

HABITAT SELECTION BY BREEDING BIRDS IN  
PONDEROSA PINE FORESTS WITH DIFFERENT  
UNDERSTORIES, MONUMENT CANYON RESEARCH  
NATURAL AREA, NEW MEXICO

by  
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## INTRODUCTION

Birds are not randomly distributed in space. No one would expect to see a Brown Creeper in a grassland or a Horned Lark in a deep woods. Any bird's two principal, sometimes conflicting, goals in life are to survive and to reproduce. In order to survive and reproduce for a time the individual must obtain certain requisities. The most crucial of these, food, shelter, and nest sites (Balda 1975), have been called "ultimate factors," because ultimately they limit survival and reproductive success.

The nonrandom distribution of birds is a result of habitat selection, the evolved tendency of individuals of each species to settle in the kinds of places in which they can optimally obtain their requisites. The choice of a given area as appropriate is "psychological" (Lack 1933), a response to the "gestalt" presented by the vegetation and other structural components of the habitat (James 1971). These cues by which an individual recognizes an area as appropriate habitat are often called "proximate factors."

If forest managers wish to predict accurately the impacts of their management decisions on bird species they must as a first step know the ultimate factors for each species. That is, what kinds of food, shelter, and nest sites are required for a given species to select a given habitat. Finding food, and to an extent shelter and nest sites, are intimately related to the physiognomy of the area. Once the absolutely limiting habitat factors are known, finer resolution can be obtained by examining the numerical responses of individual species and groups of species to quantitative variation in individual factors.

The Monument Canyon Research Natural Area (MCRNA), on the Santa Fe National Forest in the Jemez Mountains of New Mexico, is an excellent setting in which to study habitat selection by breeding birds in a portion of the coniferous forest continuum dominated by Ponderosa Pine (Pinus ponderosa). Within a single square mile are represented four sub-types of Ponderosa Pine forest, each with a qualitatively distinct understory. Because of the proximity of these sub-types, differences in their avifaunae are likely to truly reflect habitat selection rather than geographical effects. The assemblages of bird species which nest in each are probably equilibrated with their habitats.

I undertook this study to determine how birds respond to the range of habitat variation represented on the RNA and on a thinned plot just outside the RNA. There are several levels of resolution possible in such a study. First, the entire communities of breeding species in each habitat-type may be compared. Then, "guilds" of species with similar ecological characteristics may be compared among the habitat-types. Finally, each species may be examined for its presence or absence and numerical representation in each type. These analyses will show which species are to be expected in certain types of vegetation, and for some species will suggest the ultimate factors limiting them to certain habitat-types.

#### METHODS

I conducted censuses, using the spot-mapping method, of all diurnal breeding birds in five 8-ha plots. Each plot was laid out with an acreage grid in appropriate vegetation on a 1:7920 ASCS-USDA aerial

photograph (serial 3973-98). Field maps of each plot were drawn from the photograph, enlarged, and ground checked. All the birds encountered during a single census visit were recorded in position on a separate field map. These data were transcribed to a master map for each species in each plot. Clusters of registrations of singing males, locations of nests, and other data were then used to estimate the boundaries of each territory. The number of territories in each plot was then estimated, and density figures were extrapolated.

These density estimates comprise the data base of this study. The method is crude, but it is far better than the alternative, the transect method, because it allows the researcher to become familiar with individual birds and to include other useful information such as nest sites. Appendix I contains information on difficulty of censusing for most of the species encountered on the plots.

I conducted fieldwork for this study on the following dates in 1979 February 28, March 16, April 19-22, May 1-4, May 15-18, May 29-June 1, June 18-23, July 12-13. Virtually all daylight hours were spent in the plots on those dates. Each plot was visited several times on each visit to the RNA.

#### CENSUS PLOTS

The study was conducted on and adjacent to the Monument Canyon Research Natural Area, Section 9, T18N, R3E, Sandoval County, New Mexico. The RNA is on the Jemez Springs Ranger District of the Santa Fe National Forest. Its elevation is between 2830 and 3090 meters,

The five plots represent qualitatively recognizable points along a

vegetational continuum dominated by Ponderosa Pine. The plots have ponderosa in the overstory and floristically or structurally distinct understories. One plot represents the lower limit on the continuum of several species of conifers and marks the intergradation, in community terminology, of Ponderosa Pine forest with mixed coniferous forest. Although I subscribe to the continuum concept enunciated by Gleason (1926) and refined by Whittaker (1967), I will use, for convenience, such terms as "community," "mixed coniferous forest," and "habitat-type" throughout this paper.

In a concurrent project J. Deichmann and E. Kelley studied the vegetation of the MCRNA. They recognized the same four plant associations which I represented with my four natural plots, as well as one poorly-represented shrub community which I did not study. Not all of their data were available to me at the writing of this report, so I describe the plots qualitatively here.

#### I. THIN (Thinned, formerly logged, Ponderosa Pine forest)

This plot bordered the RNA on its southeastern corner. It was logged between 1976 and 1978 (T. Skinner, pers. comm.) and apparently was thinned in 1978, as some of the slash I observed in 1979 still held green foliage. Most of the large, older trees had been removed. In the northern part of the plot slash had been piled (Plate 1 ), while in the southern part it still lay on the ground (Plate 2 ). There was one large Douglasfir (Pseudotsuga menziesii) on the plot. The ground cover was almost exclusively needle litter. No part of the plot was more than 200 m distant from the boundary of the RNA.

#### II. OAK (Ponderosa Pine with other conifers and a shrub layer of oak and other species)

The OAK plot was located on a steep, tufaceous, southeast-facing

slope along the west side of the canyon (Plates 3 and 4). Ponderosa Pines, as well as occasional Douglasfirs, White Firs (Abies concolor), Southwestern White Pines (Pinus strobiformis), Pinyon Pines (Pinus edulis), and Alligator Junipers (Juniperus deppeana), grew in an open stand on the lower slope and even among the boulders of the upper cliff. Many tall pines reached above the level of the rim, so arboreal foliage was available in all parts of the plot.

Primary species in the shrub stratum were Quercus gambellii, Q. undulata, and their hybrids. Other important shrubs were Cercocarpus montanus, Chrysothamnus nauseosus, and Philadelphus sp. Ground cover was mostly mineral material and leaf litter.

### III. OPEN (Mature Ponderosa Pine forest with groundcover of grasses)

This plot was on the flat floor of the canyon, contiguous to the southern end of OAK. Its southern boundary was the boundary of the RNA. The nearly closed canopy consisted entirely of very tall Ponderosa Pines. A few Quaking Aspens (Populus tremuloides) were present in the understory (Plate 5), and some portions supported moderately dense stands of ponderosa saplings (Plate 6). The only important shrub was Robinia neomexicana. The ground cover was principally Festuca ovina, Muhlenbergia montana, and Fragaria sp.

### IV. D.H. ("Dog-hair" stands of Ponderosa Pine saplings with open canopy of mature Ponderosa Pines)

This plot was laid out along an old road (Plate 7) near the eastern boundary of the RNA. Censusing would have been virtually impossible in the thickets without the road, which was shaded and did not produce a substantial amount of edge. The road followed a gentle ridge between two shallow valleys which deepened downstream into small ravines. The only

important plant species present was Ponderosa Pine. Trees of no other species were present. The thickets were generally dense and shady (Plate 8), with many tall pines emerging above them (Plate 9).

#### V. MIX (Ponderosa Pine - mixed coniferous forest)

This plot was on the canyon floor and its moderately steep eastern slope. Ponderosa Pine and Douglasfir were the principal canopy trees. White Fir, Southwestern White Pine, and Quaking Aspen were also represented, especially in the understory (Plate 10). In the densest forest there was no ground-cover except litter (Plate 11), but open glades (Plate 12) and aspen groves with a ground-cover of grasses and Fragaria also occurred.

The five plots are construed to define a vegetational continuum along a gradient of available soil moisture. The positions of OAK, OPEN, and MIX along the Gradient are obvious, for they represent communities on the south-facing slope, the valley floor, and the north-facing slope respectively. D.H. and THIN are special cases. Because of the shading provided by the thickets D.H. is probably moister than OPEN. Snow cover definitely persisted longer there. For these reasons D.H. is placed between OPEN and MIX on the gradient. For analogous reasons THIN is placed before OAK. The continuum probably also defines a gradient of increasing foliage volume, but I was not able to measure that important parameter.

## RESULTS AND DISCUSSION

### Historic and Geographic Effects

In this paper I hope to elucidate the habitat requirements of the birds occurring in the MCRNA, i.e., to show why what birds are where. But before a bird can respond to the fine-tuning of local habitat variation



it must be present in the region. If a tropical rain forest were suddenly to appear in central New Mexico it would be some time before a full complement of tropical species could immigrate from Mexico, or local species could evolve ways of exploiting all of the new kinds of resources. The community inhabiting such a place would be poor in species for a long time. In other words, the composition of every regional avifauna is influenced by historical and geographical factors.

While we know that surprisingly great changes in the ranges of some species have taken place even in the past 100 years (Phillips 1968, Hubbard 1979) many of these have come as a result of habitat alterations by man. The birds which have responded positively to such changes are mostly species of open habitats. Forest birds are more particular about where they live, and have not expanded much. Nevertheless, forest species probably are presently on the increase, as much previously cleared or timbered land is reforested.

On a grander time scale, the advances and retreats of glaciers during the Pleistocene produced moist pluvials and drier interpluvials. During the pluvials montane forests spread into the lowlands and provided avenues for the slow dispersal of species which would not ordinarily bridge the gaps of uninhabitable country between mountain masses. During this time the Jemez massif at the southern end of the Rocky Mountains saw pulses of Rocky Mountain species spreading southward and Mexican Highland species colonizing northward.

In still earlier times Eurasian forms invaded North America by way of Beringia and established secondary centers of radiation in various places. These taxa complimented the autochthonous elements whose lineages are American as far back as they can be traced. Mayr (1946) assigned

families now inhabiting North America to elements defined by the continents of their origins. I have produced, from my own experience and primarily from Hubbard (1978), a hypothetical list (Appendix II) of land birds expected to breed in the Jemez Mountains. This is the source avifauna from which Monument Canyon draws its bird communities. Each species is assigned to one of four categories, Old World, North American, South American, and Unanalyzed, according to the criteria of Mayr (1946: 26-27). The distribution of Jemez and MCRNA species among these elements is given in Table 1. Mayr (1946) stated that the Old World Element increases in influence north while the South American Element increases in influence southward. Both the Jemez source fauna and the MCRNA local fauna have greater affinities with the Old World than with South America. This type of analysis is fruitful for a comparison of individual study plots, and we shall return to it below (page 10).

While the Jemez avifauna is clearly dominated by families of Old World origin it must be remembered that most of the species in this element arose in the New World. Examining the faunal affinities of the individual species results in a view with potential for greater resolution. I have assigned each species in the hypothetical Jemez avifauna to a modern geographical element (Appendix II), based on its current range as described in the field guides of Robbins et al. (1966) and Peterson and Chalif (1973). These elements are defined as follows: Widespread--transcontinental or approximately so; Boreo-cordilleran--boreal forest of Canada and Alaska, thence south along the western cordilleras, but not including the Sierra Madre of Mexico; Western--western North America, but not extending significantly into Mexico; Southwestern and/or Great Basin-- limited mainly to one or both of those regions of the United States; Cordilleran--montane

areas of the western United States, in some cases northward to Alaska, in every case south significantly into central Mexico; Mexican--dominantly Mexican or more southerly.

What do these elements represent? First, they are geographic not ecologic. Second, they probably do not represent centers of origin, but rather places to which groups of species have dispersed from presumed common centers of origin. Crudely, they give us hints of the affinities of the Jemez avifauna. The distribution of Jemez and MCRNA species among these elements is given in Table 2.

The Boreo-cordilleran element is much better represented in both faunae than is the Mexican Element. Similarly, those elements north of Mexico contribute twice as many species as those which include Mexico. This is a conservative assessment since the Cordilleran Element has as much area in the U.S. as in Mexico. Clearly, these avifaunae have northern affinities, as should be expected from the geographic position of the Jemez at the southern end of the Rocky Mountains.

Comparing the MCRNA assemblage to its source fauna reveals an interesting pattern. The contribution of the Widespread group is diminished in the former, while the influence of Boreo-cordilleran and the Cordilleran Elements increases. In order to become widespread a species must be able to adapt to a variety of conditions. Such species are usually inhabitants of open habitats, places where conditions are more dynamic and frequent change in physiognomy is characteristic. The MCRNA is almost completely closed-canopy forest. Because it has been undisturbed by man since 1932 all openings have grown to trees, and species of disturbed areas find no place. Both Boreo-cordilleran and Cordilleran elements represent areas characterized by coniferous forest. The MCRNA is part of an extensive

coniferous forest. It is understandable that its avifauna should draw comparatively heavily from these two geographic elements. The geographic affinities, then, of the communities under consideration are northerly, with an emphasis on areas rich in coniferous forests.

### Structure of the Bird Communities of the MCRNA

#### Geographic affinities

Having considered briefly the origins of the bird species inhabiting the MCRNA, we will now examine more precisely the structure of the communities they form. Five plots were censused in order to sample a spectrum of sub-habitat-types within the habitat continuum dominated by Ponderosa Pine. No one should assume a priori that each plot will contain a distinct community. Furthermore, bird communities, like plant communities, are points on continua, rather than discrete entities. It is wiser to talk about the degree of difference between populations in different plots, how far apart they are on the gradient, than whether they are distinct communities. However, since past workers have done just that it will be necessary to use some of their terminology in order to compare my results to theirs.

Table 3 presents densities of breeding species in each of the five plots. The number of species and the population density from each Mayrian continental element in each plot appear in Table 4.

The thinned plot had two few species and individuals to be considered profitably in the following analysis. Values for the other four plots seem to describe gradients of the importance of Mayr's elements. Number of species from the South American Element diminishes from OAK through MIX, where the one "South American" species, the Hammond's Flycatcher,

was abundant. There is a small increase in breeding pairs from the Old World Element in the same direction. This increase is steepened when percentages are considered. But, a similar increase in Old World species is interrupted at D.H. White-breasted Nuthatches were visitors in that plot, and nested in similar habitat, so one more species might be added in other years. However, there seems to be a real inflection point in habitat suitability between OPEN and D.H. Western Bluebirds and Townsend's Solitaires, not to mention the House Wren from the North American Element, need a certain amount of open space, which is not available in the heavily-timbered D.H. and MIX. (The presence of the Western Bluebird in MIX is something of a fluke, occasioned by a good nest site at the periphery of the habitat-type.) On the other hand, the dense shade of the latter two plots is ideal for Hermit Thrushes. D.H. can support all of MIX's Old World Element except the Ruby-crowned Kinglet.

Even with the perturbations the trends are impressively consistent. Mayr (1946) mentioned the latitudinal variation in importance of the elements. This variation should be transposed onto an altitudinal gradient, with the Old World Element increasing in importance as the increase in altitude produces more northerly conditions. Snyder (1950) confirmed this prediction for plots in Colorado and Utah. Additionally, he showed that the North American Element diminished in importance with altitude. Different slope exposures produce differences in effective moisture available to the vegetation, the same effect altitudinal differences produce. As a result there is what amounts to an altitudinal gradient running from OAK through OPEN through THIN through MIX, with the advantage that all plots are spatially readily accessible to all the birds. Thus the birds presumably are where they are because of habitat factors.

Both of Snyder's findings, as well as a decrease in importance of the South American Element, were confirmed on this artificial altitudinal gradient. Haldeman et al. (1973) did not find similar trends in their study of a ponderosa forest and a fir, pine, aspen forest (equivalent to MIX of this study) in northern Arizona. The former had a more dominant Old World Element than the latter. They also compared their plots with two studied in Colorado by Snyder (1950) and two in the Chiricahua Mountains of southern Arizona, studied by Balda (1967). I extended this line of analysis to the following areas for ponderosa forest: Oregon (Gashwiler 1977), central Colorado (Hering 1948, and Winternitz 1976), and northern New Mexico (OPEN, this study). For mixed coniferous forest I added central California (Bock and Lynch 1970), Colorado (Snyder 1950, and Winternitz 1976), northern New Mexico (MIX, this study), and central Arizona (Franzreb 1977). I think it is inappropriate to compare mixed coniferous and spruce-fir habitats, as they are floristically distinct, so I have eliminated Balda's and Snyder's spruce-fir forests. My inclusion of Franzreb's unlogged plot, which contained spruces, is itself marginally appropriate. Snyder's ponderosa-Douglasfir plot, because it contained the latter species in abundance, should be considered mixed coniferous forest, and I have included it in that group. True Ponderosa Pine forest (lower montane forest in the terminology of Marr (1967)) in Boulder County, Colorado occurs at much lower elevations than those at which Snyder worked. The percentages of total species and of pairs/100 acres contributed by each element are arrayed from left to right in order of decreasing latitude in Tables 5 and 6. The only consistent trends are diminution of the influence of the Old World Element for number of species in ponderosa forest and for number of pairs/100 acres in mixed coniferous forest.

The former trend is perturbed by the high value in northern Arizona, a phenomenon which Haldeman et al. (1973) were hard put to explain. There is also a slight increase for number of species in the South American Element in ponderosa forest. In general these figures do not lead to any stirring conclusions. Local conditions and yearly variations apparently have great influence on which species show up in a given plot.

The contributions of each geographic element based on current range to the total number of species and to the number of pairs/100 acres for the five MCRNA plots are given in Table 7. There are differences aplenty among plots, but no trends emerge. These data do not make any contribution to ordering the plots, as the familial elements did.

Wiens (1975), in a massive survey of breeding communities in North American coniferous forests, felt that widespread species often numerically dominate the populations on individual plots. My findings in Monument Canyon do not support Wiens's statement. In no plot is the Widespread Element numerically superior to all others. When species dominance is assessed as Wiens did, by the percentage of total density contributed by the two most abundant species, only one widespread species is rated as dominant. It is the Gray-headed Junco, a regional representative of the widespread junco complex which probably represents only one species. Incidentally, if the junco is shifted from the Southwestern/Great Basin Element, where I placed it, to the Widespread Element, the latter is still not numerically dominant. When dominance is assessed by biomass the Widespread Element is quite dominant. (See Table 11 and discussion under Species Dominance below.)

#### Species Number

Species number is the simplest parameter of bird community structure.

The most striking result in this category for the five plots is the low value for THIN. This is the first of several indications that something is wrong there. Values for the other four plots, ranging from 13 to 18, agree with the mean of 14.0 species reported by Wiens (1975) for 17 studies in the Rocky Mountain region. The figure for OPEN compares favorably with the 11 species from 13 studies in Ponderosa Pine forest below 1800 m, summarized by Winternitz (1976: 389). However, her summaries for ponderosa forest above 1800 m and for mixed forest yield 24 species each, a number not approached in this study. Tatschl (1967) studied the birds of the nearby Sandia Mountains, a range visible from Monument Canyon. One would expect avian communities in the two places to be similar. However, he found 31 species in ponderosa forests and 35 species in mixed conifers. It is clear from the format of the presentation of his data (an annotated check-list) that his objective was a faunistic survey like Hubbard's (1965), a challenge that he met admirably well. However, some of his "plots" were huge, which results in inflated species counts because of area effects. Such plot sizes are not conducive to accurate censusing, and I do not credit his numerical estimates. The Arizonan studies already mentioned (Balda 1967, Haldeman et al. 1973, Franzreb 1977) have much higher species counts (Tables 5 and 6) than those from the Jemez.

There seems to be a small decrease in species number up the moisture gradient (Table 3). This agrees with a trend in Colorado between ponderosa-Douglasfir forest and spruce-fir forest (Snyder 1950) and in southern Arizona between pine forest and spruce-fir forest (Balda 1967, 1969) but not with the superiority in species count of a fir, pine, aspen forest to ponderosa forest in Northern Arizona (Haldeman et al. 1973). The authors of the latter study commented on the unusual nature of their finding.



### Population density

Population densities varied with species counts (Table 3). In fact, the correlation coefficient  $r$  for the two parameters was .9167 ( $p < .01$ ). The average density for the four natural plots was 285.9 pairs/km<sup>2</sup> (114.3 pairs/100 acres), lower than the mean of 367.9 pairs/km<sup>2</sup> cited by Wiens (1975). This average is intermediate among the values cited in Tables 5 and 6, but it is much lower than the densities found in the Arizonan studies. In the MCRNA, although species numbers and population densities were positively correlated, the number of pairs per species was not constant. Instead this statistic increased with the former two (Table 3).

The winter of 1978-79 was unusually severe, with both prolonged low temperatures and heavy snow cover occurring throughout the Southwest. I experienced reduced species counts and population densities in summer 1979 in several places where I had worked previously (McCallum 1979a and b, 1980a and b). I am persuaded that several species of small resident birds, Mountain Chickadees, Pygmy Nuthatches, White-breasted Nuthatches, and perhaps, by analogy, Red-breasted Nuthatches, Brown Creepers, Gray-headed Juncos and others, suffered population "crashes." In at least one area, in western New Mexico, these deficits do not appear to have been made up by the summer's reproduction. This phenomenon cannot include migratory species. However, the spring of 1979 was late, cold, and wet. When birds encounter unfavorable conditions at the time at which they usually begin to breed they sometimes do not attempt to nest. It is possible this took place in 1979. Effects of both of these phenomena may have reduced species counts and population densities in this study. This shows the weakness of a one-year study, especially one done in an off-year. Even so, there is much ecological information in these data. It

will be discussed beyond.

### Biomass density

Since energy flow is a critical component of the functioning of ecosystems and is proportional to biomass, it can be argued that biomass is a better measure than population density of the importance of a given species in an avian community. I made a biomass estimate for each species in each plot by multiplying the average weight of each species, as reported in the literature, by twice the number of pairs recorded on the plot. This ignores unpaired birds, which were not censused. It is well known that a bird's weight varies through the day, and weights of the same species from different literature sources often differed by 10% or more. The biomass estimates are thus inexact. But, so are the population estimates. The data are trustworthy when these sources of error are kept in mind.

The estimates reported here are standing crop biomass, which is merely the total mass of the avian population. Consuming biomass is a better measure when community metabolism is of interest. It reflects differences in metabolism owing to differences in weight and is computed by raising the weight of each species to the .633 power (Karr 1968) before multiplying by the population density.

Biomass estimates for all plots (Table 8) are lower than the mean of 188.0 g/ha reported by Wiens (1975) for 17 census plots in the Rocky Mountain region. All of the studies summarized in Tables 5 and 6 for which the authors supplied biomass data also had higher values. This is another indication that 1979 was an "off-year." If repeated censusing in my plots produced means close to the values for 1979 the phenomenon would be of importance to an understanding of the carrying capacities of

ecosystems in closed forests.

Standing crop biomass shows the same relationship among the five plots as population density, with one exception. MIX has an unexpectedly low biomass. The average weight of individuals in a plot shows the relative contribution of large and small birds. The values for THIN and OAK are similar (17.0 and 16.9 g) as are those for OPEN and D.H. (22.3 and 21.3 g). MIX has the lowest value (13.5 g). The low average weight of the birds in MIX is explained by an abundance of small species and an absence of large ones. But, the differences between OPEN and D.H. on one hand and THIN and OAK on the other are not attributable to different relative contributions by the size classes. It is the abundance of woodpeckers in the former two plots which increases the average weights.

Wiens and Nussbaum (1975) assigned species to one of four size classes, Tiny (< 10 g), Small (11-25 g), Medium (26-80 g), and Large (> 80 g), and compared the contributions of the size classes to each of their plots. The results of a similar analysis for the MCRNA are in Table 9. The relative adaptiveness of different body-sizes may relate to the configuration of the vegetation. The twigs of firs (found only in MIX) will not support the weight of large birds, but are ideal for kinglets and chickadees. Also, dense forests (such as MIX) do not provide much flight space for the larger, less maneuverable species. The flickers and Hairy Woodpeckers which foraged all around MIX seemed to avoid the densest parts of that plot. D.H. is completely closed in the lower strata, but there is much air space among the emergent mature pines. It was these upper strata which were used by the woodpeckers.

It is interesting to compare the relative contributions of the size classes in the MCRNA to those of the six fir and/or hemlock plots studied

by Wiens and Nussbaum (1975) in Oregon. In all of their plots Tiny birds were most numerous, while Small birds dominated all my plots except MIX. MIX probably is physiognomically more like the Oregonian plots than its companion plots in the MCRNA.

#### Species dominance

It is already apparent from Table 3 that the species are not equally abundant in a given plot. Each community is dominated by a few abundant species. A simple way of assessing degree of dominance, after Wiens (1975), is to compute the percentage contribution to the plot's total population density or biomass of the two most abundant species. Results of such an analysis are summarized in Tables 10 and 11.

Except for those of THIN, the population density values (Table 10) are much lower than Wiens's (1975) means of 25% for one species and 41% for two species. This may result from a possible population "crash," which was mentioned above. Presumably the abundant species would be even more abundant in "good" years, leading to greater dominance. On the other hand, these low dominance values may be truly characteristic of the MCRNA ecosystem. It is interesting to note that dominance tends to diminish with an increase in species number and/or population density. Also, D.H. and MIX have very similar values and are next closest to OPEN and more distant from OAK according to this parameter of community structure.

When dominance is assessed according to biomass (Table 11) some changes in ranking occur. Nevertheless small birds still assert dominance by this measure when they are very numerous. In only one case (OPEN) is the extent of two-species dominance very different when reckoned by population density and biomass. This difference is caused by the abundance

of heavy-bodied woodpeckers in OPEN.

I have made a crude assessment of importance of the species among the five plots in the RNA by giving two points for each first place finish in the dominance classifications and one point for each second place. The scores for ties are divided equally. The rankings resulting from this procedure are in Table 12. Of the six species in the density listing, four are geographically migratory and a fifth, the junco, is not strictly resident in that it does not occupy its summer territories in winter. Populations of resident species are not only more susceptible to harsh winter conditions, they may be limited as a byproduct of complex social organization related to winter territoriality. In fact, some chickadee populations are denser in winter than in summer (Glase 1973, Smith 1976).

When scores for density and biomass are summed small birds remain dominant, corroborating my comment two paragraphs above. I think most visiting ornithologists would agree that the species listed in Table 12 are the characteristic species of the RNA. Nearly all are conspicuous and widely distributed. An exception is the Western Wood Pewee, which is restricted to the OAK plot. It is aurally conspicuous in the vicinity of that plot. The above generalizations confirm at the local level Wiens's prediction (1975) that widespread species will be locally dominant. (This prediction was not confirmed locally by the Widespread geographic Element, see p.13).

Relationships among the avian communities of the plots

The data reported above show that the assemblages of birds on the plots are different in some ways. We can use these data in several

ways to show how different, or similar, the communities are. One such technique is construction of a matrix of similarity using a similarity index.

A simple, frequently-used index is the one computed with the formula  $FRF = \frac{2C}{A+B}$ , where C is the number of species in common and A and B are the total numbers of species in each of the two plots. I first encountered this index in Armstrong (1972), although many other sources could be cited for it. Table 13 is a matrix of similarity using this formula.

FRF takes account of species only, and thus is purely faunistic. A more nearly exact comparison results from including quantitative data, resulting in the formula  $IS = \frac{2\sum W}{A+B}$ , as presented by Bond (1957). W is the lesser quantitative value of each species which occurs in both plots. Table 14 is a matrix of similarity using this formula.

E.P. Odum (1950) took a rather different approach. He computed a "percentage difference" for two plots by summing the differences in densities for all species in the two plots and dividing this quantity by the total densities of the two plots. I converted Odum's measure to "percentage similarity" by subtracting the difference measure from unity. Table 15 is a matrix of these measures. I used pairs/100 acres as the density measure in both the Odum and Bond procedures.

First, it is obvious that the three measures give very similar results. This is confirmed by Table 16, which ranks the dyads according to magnitude of similarity. The remarkable similarity of Tables 14 and 15, especially considering that the two indices use different information, leads me to believe that these matrices contain some biological, as well as statistical, truth. The following discussion

will refer primarily to Tables 14 and 15.

The plots have been ordered according to what I perceive to be a moisture gradient. The ordination is on habitat factors and is independent of the avian communities that inhabit the plots. If the ordination is correct faunistically each plot should have higher indices of similarity with the one or two adjacent plots than with the others. This prediction is not confirmed in all cases. THIN is by all three measures more similar to OPEN than to OAK. OPEN is more similar to MIX than to OAK by all measures. MIX is more similar to OPEN than to D.H. by two measures.

All of THIN's species are also found in OAK and OPEN, so the reason THIN is more "similar" to OPEN is simply that there are fewer additional species in OPEN than in OAK. This is another indication of the unusual nature of THIN. Table 16 shows that all the discrepancies are caused by each plot's being more similar to OPEN than to any other plot. This implies that OPEN possesses the largest complement of the regional Ponderosa Pine forest avifauna. That OPEN physiognomically is closest to the gestalt for climax ponderosa forest seem to confirm this view. Following this line of thought we might say that the peripheral communities (the other plots) borrow from the avian communities of adjacent plant community types.

Some workers consider that a similarity-index value of less than .500 delimits two separate communities. By this criterion my study area would possess three breeding bird communities, one represented in THIN, one in OAK, and one in OPEN-D.H.-MIX. Of course THIN does not possess a distinctive assemblage of species. The low indices result from the poverty of its species count. OAK, however, does appear quite different from the remaining three plots. My speculations on the

reasons for this appear in the section Character of the Assemblage of Species on Each Plot (p.27). MIX represents what is usually considered a different plant association, mixed coniferous forest. Ponderosa Pine is present in the plot, but it is not as dominant as in the other plots. Yet the avifauna of this plot is very similar to that of typical OPEN Ponderosa Pine forest. Haldeman et al. (1973) studied a plot in an area of more extensive mixed coniferous forest in northern Arizona and also found the bird community to be more similar to than different from that of a nearby ponderosa forest. Reasons for the differences that do occur will be discussed below (p. 35).

#### Foraging and Nesting Guilds

It may be easier to appreciate the differences among the plots by looking in more detail at the ecological requirements of the species which nest there. Following Salt (1957) and Bock and Lynch (1969), I have assigned each species to a foraging "guild," on the basis of where and how or on what the species feeds during the breeding season. Since I suspect that availability of nest sites often has as much influence as availability of food and foraging sites I have also assigned each species to a nest-site guild. The Cavity-I category refers to species which usually excavate their own cavities, and Cavity-II to those which usually use natural cavities or those excavated by other species. My assignments to these categories are in Table 17.

Table 18 shows the relative contribution of each of the foraging guilds to the total population density and total biomass of each plot. Wiens (1978) reported that foliage-foragers comprise more than half the avian populations of Rocky Mountain coniferous forests, as well as of coniferous forests in other regions of North America. Foliage-feeders



do not approach this dominance in the MCRNA. In fact, foliage-feeders are dominant in only OAK (by numbers and biomass) and OPEN (by numbers). In general, the birds in each plot are fairly well distributed among the foraging guilds. The Ground-Insect category is dominant by weight in three plots. Three plots contained no nesting nectar-feeders. D.H. and MIX are so densely shaded that few herbaceous plants grew there. THIN is very open but still possessed few herbaceous plants, perhaps because of soil acidity, a factor that may also affect D.H. and MIX. Neither THIN nor OAK had timber-drillers, although both were visited by these birds. Perhaps better nesting sites existed in other habitat-types. In extensive thinned and pine-oak stands woodpeckers are probably present in small numbers. THIN had no members of the Hawking guild (flycatchers). It does not have the tall snags required by Olive-sided Flycatchers or the shrubs required by Dusky Flycatchers. Hammond's Flycatchers were aurally conspicuous in adjacent "dog-hair" stands. Their absence must result from the canopy's being too open.

Table 19 shows the contribution of each nesting guild to the plots. Most of the ground-nesters and cavity-nesters are obligately so, although some of the latter (nuthatches, chickadees) may qualify for both subdivisions of that category. Foliage-nesters are more variable, as the three subdivisions reflect primarily differences in height preferences. The most striking result of this analysis is the absence of foliage-nesters from THIN. Although it may be less abundant than in other plots, foliage is present there. Except for a few emergent trees the canopy in THIN is at the level of understory in the other plots. These small trees are widely spaced, compared to the spacing which existed before thinning, a condition that persists in D.H., where several species nested

in the foliage. Moreover, one part of THIN does have a rather dense overstory. It obviously supported no foliage-nesters. Shrub-nesters were absent in the deeply shaded MIX and D.H. plots, where no shrubs occur.

Foliage-nesters contributed nearly twice the percentage of birds in OAK that they did in OPEN and D.H. On the other hand, cavity-nesters made more than twice the contribution in the latter two plots that they did in OAK. Most of these differences can be explained in terms of how well each plot supplied the requisites of each species. I shall defer discussion of this subject to another section (p. 33).

### Snags

Balda (1975) and Jackman (1974), among others, have emphasized the importance of snags as nesting sites. Table 19 shows that cavity-nesters are numerically important in several plots on the MCRNA. I counted all dead trees, including aspens, in each plot. Table 20 presents the number of cavity-nesters and of snags in each plot. There is no correlation between the two measures ( $r = -0.0669$ ,  $p > .05$ ). The importance of snags to each plot will be discussed below.

### Gradient Analysis of Bird Populations

The results presented above show how different the assemblages of birds on the five plots are. I stop short at designating any of these assemblages community-types, or facies of community types, because I do not believe discrete community-types exist. Individual species have unique requirements and are spaced along resource gradients in different patterns. This is the continuum concept of Gleason (1926) which has been thoroughly explicated by Whittaker (1967). Bond (1957) showed the

usefulness of the concept for studies of avian communities. More recently, several workers (e.g. Shugart et al. 1975, K. Smith 1977) have endorsed the concept with their multivariate assessments of realized avian niches.

Figure 1 shows graphically the rise and fall of the population density of each species along the moisture gradient represented by the five plots. Two limitations of this presentation should be kept in mind. One is that since there are no replicates of the several points on the continuum each value is subject to local idiosyncrasies. An average of values from several similar plots would have been preferable. The second problem is that the ordination of the plots on the continuum is intuitive, and the distances between plots on the X-axis are artificial. Nevertheless, I believe most visitors to the plots would agree that they have been ordered correctly according to increasing soil moisture and perhaps increasing density of the canopy.

Figure 1A shows the densities of species restricted to one plot. Only OAK and MIX possessed such species. This implies that the two plots have relatively distinct bird communities, and is correlative with the low similarity indices for this dyad. The OAK-MIX dyad ranked lowest in two of three comparisons (Table 16). In fact, only the five widespread species (Fig. 1, parts E and F) and the White-breasted Nuthatch, which is widespread geographically and variable ecologically, occur in both plots. It is to be expected that plots at opposite ends of a gradient will have these characteristics.

The species shown in Fig. 1A are restricted to one plot for different reasons. The Dusky Flycatcher, Virginia's Warbler, Olive-sided Flycatcher, Ruby-crowned Kinglet, and Warbling Vireo respond to specific habitat features unique to the plots they occupied and did not even visit other plots during the breeding season. The other species were less specific

in their requirements. One of these, the Mountain Chickadee, was unique as a result of rarity rather than habitat selection.

The dichotomy between ends of the gradient is further emphasized by Fig. 1, parts B and C. Figure 1B includes species restricted to the upper end of the gradient. These are evidently kinds which require shady, closed forests. Natural history data on the individual species confirm such an assessment. Figure 1C depicts a group of three species which require open conditions or easy access to the ground. Both the bluebird and the solitaire frequently forage by pitching to the ground from an exposed perch. The wren forages in brush and slash near the ground. Despite the avifaunal impoverishment of THIN it is well-represented in this ground-oriented group. Only one species (Broad-tailed Hummingbird) which goes no further up the gradient than OPEN is not found in THIN.

Figure 1D depicts an assortment of species which spurn the extremes of the gradient. The figure may imply that the entire ecological ranges of these species are included within this section of gradient, but this is not the case. Reasons for the abbreviated distributions are idiosyncratic and will be discussed below. Parts E and F of Figure 1 show the densities of species found in four or five of the plots. Two patterns emerge, one a steady climb up the gradient punctuated by a fall at MIX, and one a steady fall from OAK or OPEN to MIX. The widespread Gray-headed Junco shows no pattern.

Ideally the gradient should include the entire ecological range of the species. The abundance curve would then be low in marginally acceptable habitats and rise to a peak or peaks in optimal habitats. A critical assumption here is that birds respond numerically to differences in the quality of habitat. This may not always be the case, but the assumption is usually made in this kind of analysis. Importance values may be

substituted for densities.

The gradient represented by my study plots is not an extensive one. It does not span the entire distribution of any of the bird species found on it. Moreover, because the censuses were not replicated it is not wise to place great emphasis on the population densities. Even so, gradient analysis can contribute much to our understanding of habitat selection on the MCRNA. The plots were chosen to represent minor, but recognizable, variations in the understory of Ponderosa Pine forests. Comparisons among the plots amount to sets of controlled experiments for the effects of various habitat factors on the presence and absence of a given species. Gradient analysis refines such an approach by emphasizing continuities, discontinuities, and peaks in abundance.

The synthetic treatment which follows will draw on all the results presented above, especially the guild and gradient analyses, and experience and intuition, in its speculations on why which birds were where.

#### Character of the Assemblage of Species on Each Plot

##### THIN

THIN's avifauna is a subset of that of either OAK or OPEN. All its species are found in both those plots. Because THIN and all other plots except OAK lack a significant shrub stratum and the birds characteristic of such vegetation it is safe to assume that THIN is most closely related to OPEN. Indeed, I decided to study a thinned area to test the hypothesis that artificially and naturally produced open Ponderosa Pine forests, being structurally similar, support the same bird community. In fact there were some major structural dissimilarities between the two plots. THIN has very few standing snags. The canopy in OPEN is much higher;

that of THIN is really a remnant subcanopy of small trees. There are few tall trees on the plot, most of them having been removed by lumbering. THIN has a temporary artificial "shrub stratum" of piled slash. Finally, OPEN has a well-developed herbaceous ground cover. The groundcover of THIN, and of D.H., is almost completely needle litter. THIN is essentially and developmentally D.H., minus snags and some of the tall trees.

THIN is characterized by birds adapted to the ground and to tree trunks. Three of five ground-feeders had territories on the plot, and a fourth, the flicker, visited there. The total density of these was comparable to that of the Ground-Insect guild on other plots. Cavity-nesters were also important, but less so than in any other plot except MIX. THIN should be good habitat for woodpeckers, nuthatches and swallows, all of which like relatively open woods. Had there been more dead snags available for nest sites Pygmy Nuthatches and Violet-green Swallows might well have been abundant, and Common Flickers, Williamson's Sapsuckers, and Hairy Woodpeckers might have been residents rather than visitors. As it was, the real ability of the plot to support cavity-nesters is over-stated, because one pair of bluebirds and two of Pygmy Nuthatches nested off the plot but maintained partial "territories" on it for feeding. There were only ten snags on the plot. (The most important of these, which contained a nuthatch nest and a swallow nest, was cut down illegally after the nesting season.)

Members of the foliage-foraging and foliage-nesting guilds were notably absent or rare on the plot. Many such species visited the plot, and a Grace's Warbler had a partial territory there. The Hermit Thrush was merely a vagrant from contiguous "dog-hair" stands, but all others conceivably found appropriate foraging zones on the plot. Two hypotheses, which are not mutually exclusive, offer explanations for their failure to

breed. Foraging substrate, and thus food, may have been adequate structurally but so widely distributed in space that breeding was not energetically feasible. In other words, the visitors were non-breeding individuals wandering through subminimal habitat rather than visiting breeders from adjacent territories. Also, suitable nesting sites may not have existed. In this case the openness of the canopy is implicated. Perhaps the proper gestalt, the constellation of clues by which birds recognize that a territory will provide the proper kind of nesting site and sufficient food to raise a family, is missing.

Of the visitors I would most expect the Common nighthawk, Brown-headed Cowbird, and Western Wood Pewee to breed on the plot. The former two would have given the plot some unique species, which its position on the xeric extremity of the gradient merits. The nighthawk was heard commonly in the vicinity and may indeed have nested on the plot. My records were not sufficiently numerous for me to make that judgement. Cowbirds could hardly nest where there were no foliage-nesting birds to parasitize. The absence of pewees is harder to explain. In the OAK plot they characteristically hunted from the dead lower limbs of large pines. They also saddle their small nests on such limbs. Perhaps the absence of large dead lower limbs on the young trees which characterize the plot is the reason pewees did not nest there.

The Hammond's Flycatcher, Brown Creeper, and Steller's Jay, all of which inhabit OPEN, are near the lower limit of habitat suitability there (Fig. 1B). That plot's nearly-closed canopy makes it sufficiently mesic for these species, which are found up the gradient in much more mesic situations.

Thus, artificial opening of a "dog-hair" stand has not produced a man-made equivalent of open Ponderosa Pine forest, at least not immediately.

The last thinning of the plot was apparently in 1978, one year before the census. The plot's avifauna simply may not have equilibrated in the single year since manipulation. Most bird species are tenaciously faithful to previous years' nesting territories. Perhaps the plot's residents abandoned the area in 1978, and because of generally low densities in 1979 new individuals were not available to colonize this new habitat. The only way to answer questions of this sort is to conduct a color-banding study to assess the fates of individual birds immediately before, during, and after logging and thinning. Such a study is vitally needed to assess the true impacts of forest management on bird populations.

Despite the possibility that THIN will equilibrate and support more birds, my judgement is that it will not, at least for some time. It is too open and even-aged to be colonized by many of the species present at its elevation and too far from open country to be colonized by species which might prefer such openness. Franzreb (1977) and Bock and Lynch (1970) found that some species responded with denser populations to the opening of coniferous forests. Of the ten species in Franzreb's study which benefitted from heavy overstory removal six were found in the MCRNA. Four of these had territories in THIN, but none was more abundant there than in the unmanipulated plots.

#### OAK

OAK had the most distinctive assemblage of breeding birds of any plot. It had six unique species and the lowest average similarity indices (.5058 for FRF). It differed from OPEN, it's "nearest neighbor," in having 22.5 foliage-nesters (66 percent of the total) to 8.5 (35 percent) for the latter plot. There was a corresponding relative unimportance of cavity-nesting species in OAK.



OAK also had much higher percentages of foliage-foragers and fly-catching birds than OPEN, especially when biomass is the medium of comparison. The discrepancy is made up by OPEN largely in the Timber-Drilling and Timber-Probing guilds.

Of the species unique to OAK three were responding there to identifiable requisites which are available in no other plot. For Virginia's Warblers and Dusky Flycatchers this requisite is a well-developed shrub stratum. Virginia's Warblers characteristically nest on the ground, among the roots of oak, mountain mahogany, or other large woody shrubs (Johnson 1976, Hubbard 1965, Tatschl 1967). They forage among the leaves of these shrubs (Marshall 1957) rather than in the conifers which usually accompany them. Dusky Flycatchers nest close to the ground. Oaks, junipers, and small aspens are preferred sites. Male duskies may sing and call from the tops of tall trees, but foraging is usually done below the canopy. I consider nest sites to be the limiting factor for Dusky Flycatchers in the MCRNA. In the three plots with denser canopies the closely related Hammond's Flycatcher occurred. Habitat selection in Empidonax flycatchers is rather strict, and interspecific territoriality sometimes occurs (Johnson 1963). The two species were so faithful to habitat-type in the MCRNA that I had no opportunity to see if they practiced interspecific territoriality.

In the MCRNA the Olive-sided Flycatcher is limited to areas with tall snags and steep slopes. In general it is a species of tall, isolated trees (Salt 1957, Kilgore 1971, Phillips 1937, pers. obs.). Tall, isolated trees occur in D.H., but that plot is only gently rolling, unlike the steep north slope of the RNA and OAK, where the species occurred. It is interesting that the latter two places are quite different floristically, and that these flycatchers usually inhabit sites more mesic than

OAK.

As noted above the Western Wood Pewee likes to hunt from dead lower branches of pines. This requirement would seem to be met in OPEN, but the abundance of pewees in OAK implies there is something about its vegetation that is distinctly preferable to OPEN's. Perhaps the cathedral-like canopy of OPEN is too high and closed for pewees. OPEN has few limbs at the level frequented by pewees in OAK.

There is no obvious explanation for the limitation of Western Tanagers and Black-headed Grosbeaks to OAK. Both species occur in a variety of vegetation-types in different parts of their ranges. The grosbeak may have a preference for broad-leafed vegetation. These are species of open situations, however, and D.H. and MIX are clearly too closed for them.

Solitary Vireos and Grace's Warblers, both foliage-gleaners and foliage-nesters, reached density maxima in OAK. They probably were not responding to the shrub layer at all, but to the openness of the canopy. Although not too much faith should be put in the density estimates, and the vireo occurs in other kinds of vegetation, it is safe to say that moderately open pine forest is more suitable for these species than those types represented by the extremities of the gradient.

The Acorn Woodpecker (Melanerpes formicivorus) and the Rufous-sided Towhee (Pipilo erythrophthalmus) are two species for which OAK seems to be excellent habitat. Probably an area effect rather than ecological inappropriateness explains their absence. OAK is a small patch of pine-oak vegetation, surrounded by large areas without shrubs. Thus, although OAK has the greatest number of species of the five plots, it is depauperate in oak-related species. This impoverishment is related to dispersal and extinction according to the hypothesis of island biogeography (MacArthur and Wilson 1967). The same is true for MIX.

The reason for the low number of cavity-nesters is not paucity of snags, for OAK has more than OPEN. (Table 20). Nor could it conceivably be related to the high number of foliage-nesters, since they are for the most part in different foraging as well as nesting guilds. An explanation must be sought in the individual preferences of each species.

Violet-green Swallows frequently nest in tall pine snags, which were present and used by other species on the plot. Swallows were common over the plot throughout the breeding season, and were seen gathering nesting material on it. Nevertheless, I found no nests. It is possible that these swallows nested in natural cavities and crevices in the tuff cliffs, as they do in some other places. Otherwise their apparent rarity cannot be explained, unless there is an absence of woodpecker holes.

All four species of woodpeckers which I found regularly in the MCRNA visited the OAK plot, but none nested there. It was my judgement that all but the flicker made sufficiently little use of it for it not to be considered part of their territories. The Williamson's Sapsucker and the Hairy Woodpecker were clearly drawn to the aspens in OPEN. Since these species did not have contiguous territories, intraspecifically, in the MCRNA, it was simply a case of their establishing territories around the best nest sites. In an extensive pine-oak woodland Hairy Woodpeckers would be likely to occur. I have seen Williamson's Sapsuckers in dry pine forests but they may not nest in them. They seem to require aspens for nesting (Crockett and Hadow 1975).

#### OPEN

It is already clear that OPEN is the "average" plot in the continuum I studied at Monument Canyon. I might even say that it possessed a "typical" Southwestern Ponderosa Pine forest avifauna. This is an unwary statement,

since I have argued that constraints on dispersal and local peculiarities have an important effect on which birds are where. Nevertheless, some species always come to mind when one thinks of ponderosas, and these, for example the Pygmy Nuthatch, Mountain Chickadee (Although absent in 1979 it is presumably present most years.), Grace's Warbler, Steller's Jay, and Solitary Vireo, are here.

If the densities in Fig. 1 may be trusted to indicate which plot represents optimal habitat, it appears that "average" is not "optimal" in many cases. Densities are highest in OPEN for only three species. On the other hand, seven species are at a terminus of acceptable conditions there. The plot is just open enough for Townsend's Solitaires, Western Bluebirds, and House Wrens, the latter two of which benefitted from opening of the forest in Franzreb's study (1977). On the other hand, the forest appears to be just dense enough for Hammond's Flycatchers, Steller's Jays, Williamson's Sapsuckers, and Brown Creepers. Creepers and solitaires were adversely affected by logging in Franzreb's study. It is noteworthy that all four of the latter group made some use, as visitors, of the more open OAK plot, while only one of the former group, the solitaire, visited the densely wooded D.H. The bluebird's presence in MIX is a special case related to a nest site.

The OPEN plot is importantly atypical in one respect. It contains a few aspen trees, and there is a small grove just outside the plot. These trees have a profound effect on the composition of the avian community of the plot. Aspen wood is soft and easily excavated. Most woodpecker species use aspens for nesting when it is available. Four aspen trees within 1/16 ha contained the nests of pairs of Hairy Woodpeckers, Western Bluebirds, House Wrens, and Violet-green Swallows. Williamson's Sapsuckers nested nearby, presumably in an aspen, and Pygmy Nuthatches and flickers

nested in pines within 30 m of the aspens. Frequent interspecific hostility among these species, especially the Hairy Woodpeckers and bluebirds, attests the importance of these nest sites. Franzreb (1976) described hostility between Mountain Chickadees and Violet-green Swallows over an aspen nest cavity.

One foliage-nester, the Warbling Vireo, seems to be dependent on aspen in the MCRNA. It was found only in a dense aspen grove in MIX and in the small aspen grove adjacent to OPEN.

The absence of Yellow-rumped Warblers, Western Tanagers, and Black-headed Grosbeaks is difficult to explain. The latter two were uncommon or absent in other studies I consulted, so their distributions typically may be patchy. The grosbeak may also prefer territories with more deciduous vegetation than OPEN can offer. But the warbler was present in all other pine forests with which I have compared this plot (Table 5). It is perhaps relevant that the species was nowhere abundant on the MCRNA in 1979. The Western Wood Pewee was discussed above.

D.H.

"Dog-hair" stands comprise the most abundant and most conspicuous floristic element of the MCRNA. They look wild, with many snags and large trees rising above the virtually impenetrable thickets of even-aged saplings. R.P. Balda has said (D. Smith 1975:87), "I know of no species that is restricted to or makes any significant use of thickets." I began this study with a similar orientation, but curious as to just how OPEN and D.H. would differ.

The differences were not dramatic, as Table 3 shows. Only six species were not shared by the two plots, and two of those may occur both places in some years. There is not much difference in the percentage contributions

of the nesting guilds (Table 19). Foraging guilds show more differences (Table 18). On a percentage basis aerial and timber-foragers are more important in D.H. and hawkers and foliage-feeders are more important in OPEN. This is understandable since there is much air space above the thickets and an abundance of bark surfaces in D.H., while the thickets impede the movements of foliage-gleaners and sub-canopy hawkers.

The presence of thickets does produce some structural differences that are recognized by a few species of birds. The thickets are clearly inappropriate for foraging by bluebirds and House Wrens. Wrens like brush piles and shrubs; cover is not properly concentrated for them in D.H. Another ground-forager, the Townsend's Solitaire, was seen in D.H. several times and may have nested there. Hermit Thrushes occur in MIX and D.H., but not in OPEN. Presumably the thickets produce enough close-to-the-ground shade to approximate the conditions of their favored mixed coniferous forests and enable them to expand into this different habitat-type. This is the most unambiguous example in this study of a species responding to the structure rather than the composition of the vegetation.

It is with density measures that the most important distinctions arise. OPEN had 56 percent more individuals and 62 percent more biomass than D.H. Only two species were numerically superior in D.H. These, the Violet-green Swallow and the Pygmy Nuthatch, reached their highest densities on this plot, and are responsible for the high showings of their guilds. The nuthatch also made heavy use of the thickets in winter. These results seem to contradict Balda's statement. However, he was undoubtedly speaking of thickets lacking a canopy of emergent living and dead trees. This is the limiting resource for these two species and for all cavity-nesters. Despite the rich foraging zones there would not have

been a single nesting nuthatch or swallow in the "dog-hair" stands without the old trees, because none of the saplings are big enough for a suitable nest cavity. The same may be said for Hairy Woodpeckers, flickers, probably creepers, and chickadees, White-breasted Nuthatches, and Northern Three-toed Woodpeckers. The latter three species, although not recorded as breeders on the plot, used "dog-hair" stands elsewhere on the MCRNA. The Hermit Thrush, a colonizer from mixed coniferous forests, may even need these as well as the dense shade produced by the thickets. The males of this species typically sing from exposed perches and might pass up areas lacking good song-posts.

Despite faunistic similarity to OPEN and MIX, D.H. is inferior to both in number of species, population density, and biomass. It is clearly only a fair approximation of either habitat-type, as far as the birds are concerned. On the other hand, and this is perhaps the most surprising and important finding of this study, it is far superior by all these measures to THIN. This is perhaps an unfair comparison, since THIN is virtually snagless, but even with such a disclaimer D.H. seems superior and more productive habitat just because of its contingent from the foliage-nesting guild. It should be mentioned, however, that three of these, the vireo, flycatcher, and Grace's Warbler, were concentrated in a corner of the plot where the thickets were rather less dense than elsewhere. The Yellow-rumped Warbler, on the other hand, seemed to prefer the thickets.

#### MIX

This plot was chosen as a representative of mixed coniferous forest, an assemblage of tree species which, because of its floristic and physiognomic distinctiveness, is considered by many to be a plant community

distance from Ponderosa Pine forest. It is the Canadian life zone of Merriam, while the four other plots would be called Transition zone communities. As my results, and those of Haldeman et al. (1973) show, however, it is not perceived as very different by the birds.

This plot, in 1979, had three breeding species not found in any other plot. One of these, the Mountain Chickadee, is sometimes the most common species in ponderosa forest. However, it was rare in 1979. Its restriction to MIX was purely a matter of chance and had nothing to do with habitat selection. The Warbling Vireo was present because the plot contains aspens. The Ruby-crowned Kinglet is the only species which apparently keyed on the broad-needled trees which distinguish this plot from the others.

Two species which prefer more open situations were recorded on the plot because they nested in an aspen grove near its periphery. They were clearly attracted to the nest sites, and I never saw them forage in the densely-wooded parts of the plot. They are the Williamson's Sapsucker and the Western Bluebird. When the sapsucker is discounted it becomes apparent that woodpeckers did not make extensive use of the dense forest characteristic of the plot. Hairy Woodpeckers, sapsuckers, and flickers were all frequently encountered in the more open forest surrounding the plot but seldom within it.

Hammond's Flycatchers were especially abundant in MIX, but they were chiefly encountered in the more open parts of the plot. The densest parts were used little by species other than the Hermit Thrush and the Ruby-crowned Kinglet.

Haldeman et al. (1973) found more individuals and species in mixed coniferous forest than in Ponderosa Pine forest. Perhaps I would have



found a similar relationship had the MIX plot not been such a small and isolated patch of mixed coniferous forest. The Red-breasted Nuthatch is one species typical of mixed conifers which was inexplicably absent from this plot and from a larger area of similar vegetation on the north slope of Section 9. If these areas had been more extensive they might also have included some spruce-fir birds.

#### MANAGEMENT IMPLICATIONS

Following the theoretical work of MacArthur and subsequent field investigations of the concept (see MacArthur 1972:169-194 for review), "bird species diversity" has attracted much attention among ecologists and resource managers. The Symposium on Management of Forest and Range Habitats for Nongame Birds, sponsored by the Forest Service in 1975, was the scene of much discussion on the subject of managing for maximum diversity. In general, the managers present seemed to favor the idea, while the academicians, who were largely responsible for the data presented at the meeting, deplored the idea. The dichotomy in opinion is easy to understand. Managers, who have many other pressing responsibilities, desire a simple measure of the success of their efforts. Academicians tend to be concerned about the birds themselves and to prefer unmodified ecosystems.

I do not intend to refute the concept of species diversity, but a word to the wise on its staying power is in order. Robert MacArthur was a brilliant intuitive naturalist with a mathematical bent. He has been widely credited with introducing the hypothetico-deductive approach of the harder sciences to ecology, a discipline which was mired in descriptivism. His hypotheses, for example those on island biogeo-

graphy, species diversity, and patchiness, inspired a tremendous amount of fieldwork. Some studies confirmed his predictions, others did not. Some workers arranged and rearranged their data until they conformed to theory. For example, a correlation between foliage height diversity and bird species diversity came to be accepted as gospel and some researchers sought the optimal layering of foliage for the desired correlation. Mathematical ecologists have produced diversity index after diversity index and each in turn has been shown to be inadequate in one way or another. One worker (Hurlbert 1971) even declared species diversity a "nonconcept."

Furthermore, evolutionary theory is currently in flux. Competition is one of the concepts which is in question in some quarters (Wiens 1977), and strong competition is a fundamental assumption of the ecological theory of the MacArthurian school. I have no doubt that were MacArthur alive today he would be in the vanguard of those questioning his earlier ideas, leaving some of his followers behind in outmoded orthodoxy, as men of genius often do. It would be unfortunate for managers to pin their hopes on a relatively new concept, which by the time the success of their management efforts can be assessed, may have been abandoned by its originators. I urge a more conservative approach.

The keys to the integrity of coniferous forest avian communities are old-growth stands and the larger bird species. For some species very mature forests may be an absolute requisite. The Ivory-billed Woodpecker (Campephilus principalis) is an obvious example. The Boreal Owl (Aegolius funereus), Spotted Owl (Strix occidentalis), and Pileated Woodpecker (Dryocopus pileatus) have been suggested as species dependent on old-growth coniferous forests (Thomas et al. 1975). The way to

identify such stenoeconomic species is through autecological studies.

The needs of large, wide-ranging species are not accurately assessed by community studies such as this one. For example, I was not able to assess the importance of the Goshawk to the ecosystem I studied. A management plan which considered the data presented here but ignored the Goshawk might result in the destruction of a resource essential to the presence of that species. Diversity indices and the like will never be able to provide that kind of information. The only way to assess potential impacts on Goshawks is to study Goshawks specifically.

Once the needs of large species and those restricted to old-growth forests are attended to the manager concerned with the impact of his decisions on the more common, more adaptable species might turn to a study such as this one for guidance. His first concern should be snags. Balda (1975) pointed out that most winter residents of Ponderosa Pine forests are insectivores and cavity-nesters. These birds can have a profound positive effect on the health of the forest, as they tend to prevent epidemics of insect infestation from occurring (Bruns 1960).

Although there is no correlation between the number of snags and the number of cavity-nesters on the plots, it must be remembered that population densities were low in the one year of this study. In other words, populations may not have been limited by nest-site availability. As Balda (1975) astutely noted, if you leave only enough snags to support a depressed population of cavity-nesters, you limit populations to these sub-optimal levels for a long time to come. If the Forest Service policy on leaving snags is followed there is hope for cavity-nesters. The snag policy has not been successfully prosecuted in THIN, however. Perhaps most snags were removed when the timber was harvested,

before the snag policy went into effect. Perhaps the remaining ones were cut illegally, as was the large snag I mentioned on page 18 .

The next most important consideration is how much thinning should be done. It is quite possible that if more young trees had been left in THIN some species of the foliage-feeding guild may have been retained, perhaps without diminishing tree growth. The optimal amount of thinning may be different when birds are considered than when only timber production is considered. But, it may be necessary to leave more mature trees, i.e. to close the canopy somewhat, in order to retain these species. The above are speculations, but I say without hesitation that large tracts resembling THIN will be avian wastelands. Whether it is intentional or not, such management is close to tree-farming rather than multiple-use management.

In the preceeding two paragraphs I have mentioned management for the needs of specific guilds of birds. It is always best to consider impacts on individual species, for these are really the only entities which respond in an evolutionarily concerted way to habitat. (The guilds mentioned so frequently here are defined by correspondences and are coherent only so far as the correspondences go.) Moving along the gradient one might ask, how much timber can be taken out of OPEN before the Brown Creeper, the Hammond's Flycatcher, and the Steller's Jay are lost. At what point does one move irrevocably from the rich avian community of OPEN to the depauperate one of THIN?

Approaching THIN from another direction, how much may the thickets of D.H. be thinned before the Hermit Thrush drops out? As it apparently finds OPEN too open, it would appear that the thrush could tolerate very little thinning of a stand like D.H. As the vegetation is altered

some species will drop out and others may come in. An index of diversity may or may not show this, but the Hermit Thrush will definitely be gone.

Removal of aspen will remove Warbling Vireos and Williamson's Sapsuckers, even if no other change is made. Removal of "brush" will expel Virginia's Warblers, probably Dusky Flycatchers, and possibly Black-headed Grosbeaks. A forest with no dead or dying trees will have no Brown Creepers, for they will find no slabs of exfoliating bark under which to nest. Ruby-crowned Kinglets are not likely where the only conifers are Pinus and Juniperus. These are examples of species which are limited by a single factor. No kind of diversity index, nor indeed any of the phytosociological measures usually employed by plant ecologists, will reflect these absolutes, and yet they are so simple that they are easily and straightforwardly responded to. Of course once the absolute requisite is obtained most species respond numerically to quantity and quality of these and other requisites. But it is pointless to ask how many pine trees a sapsucker needs for foraging when she has no aspen to nest in.

The differences in species composition of the plots in this study show that, even within such a small and homogeneous area as the MCRNA, one will not find all the species in one place. I have tried to show some of the factors limiting these species. This should be helpful to managers in deciding how to encourage certain species, or, on the other hand, predicting what species they will have with certain policies.



Plate 1. THIN Plot.

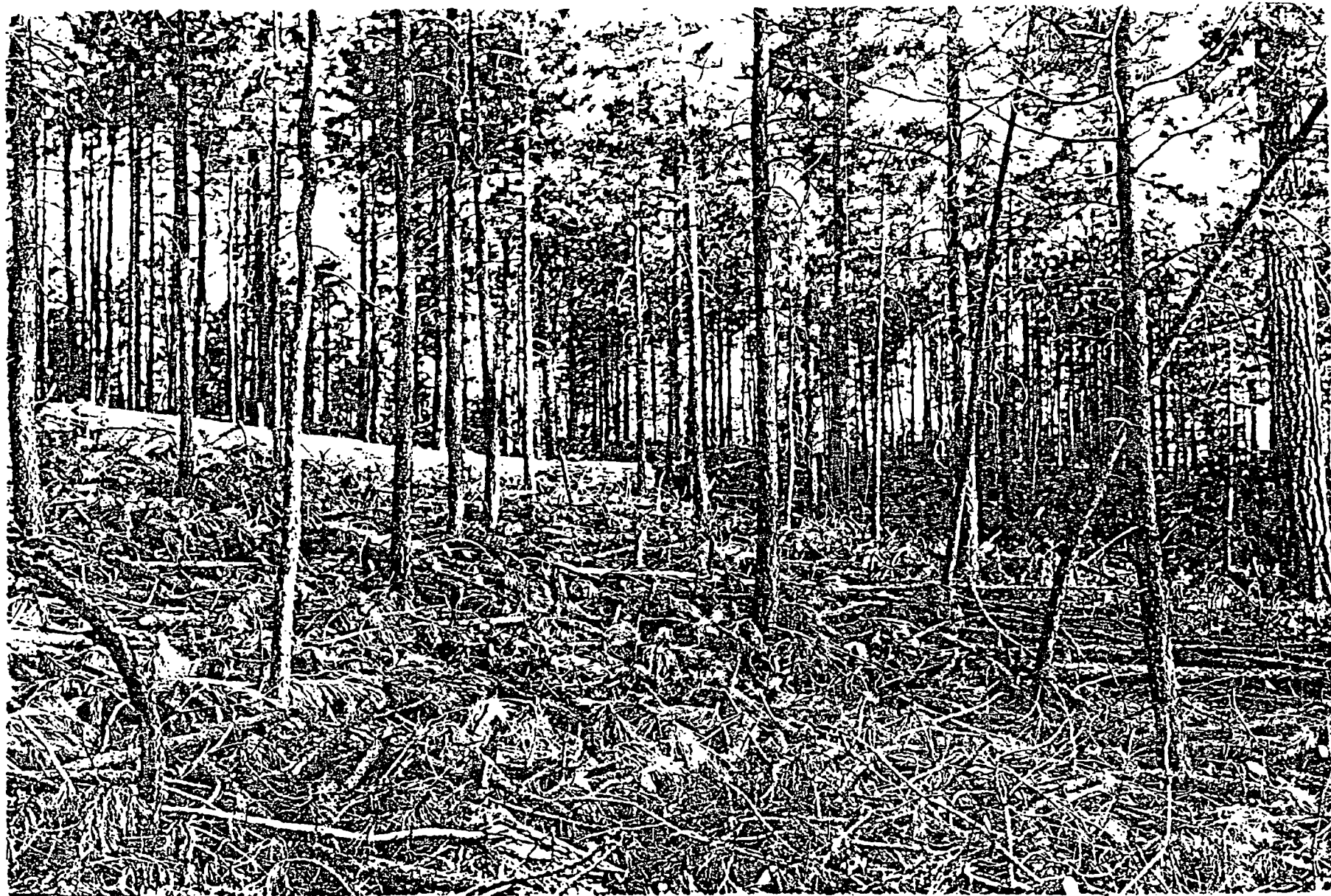


Plate 2. THIN Plot.





Plate 3. OAK Plot.





Plate 4. OAK Plot.

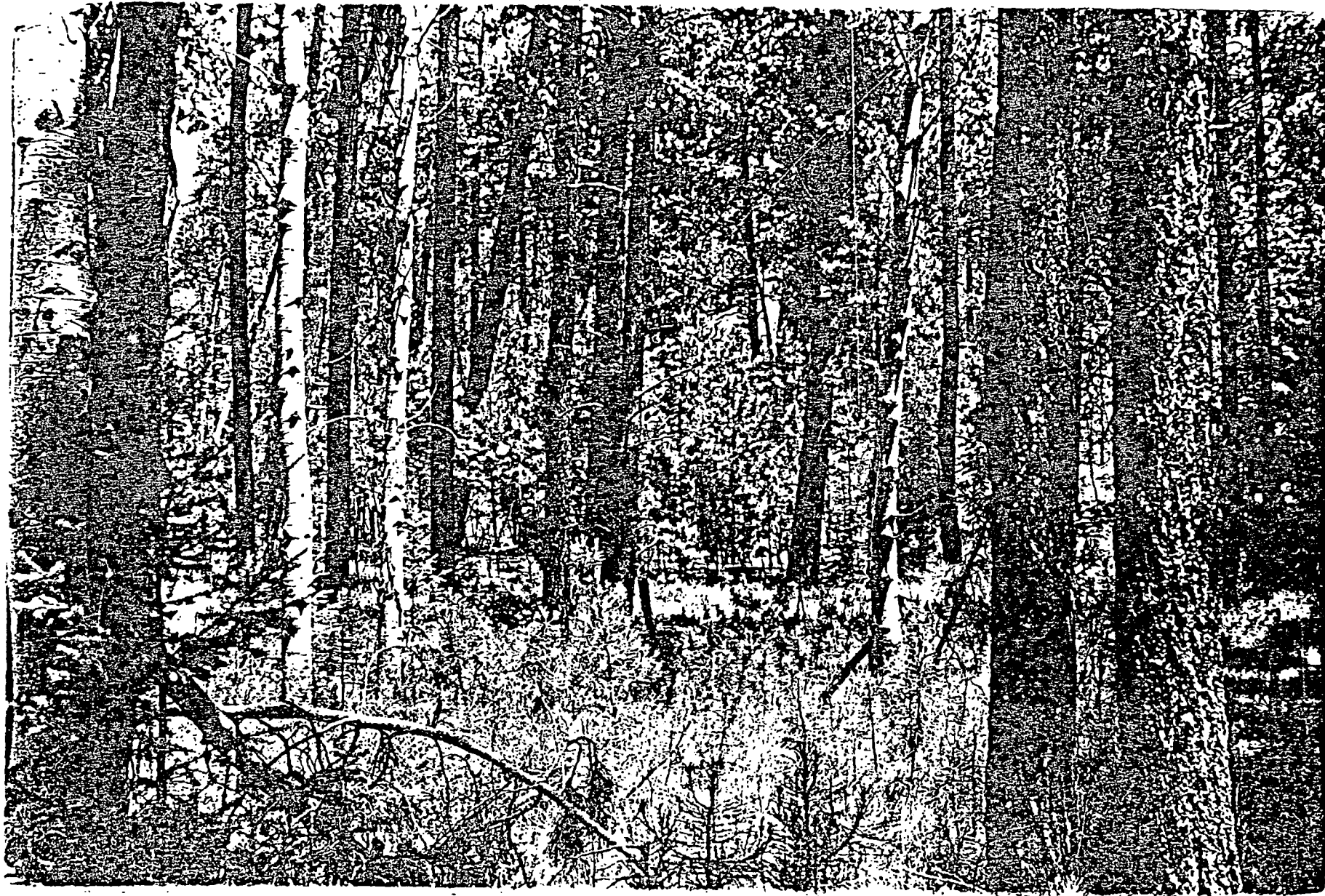


Plate 5. OPEN Plot.

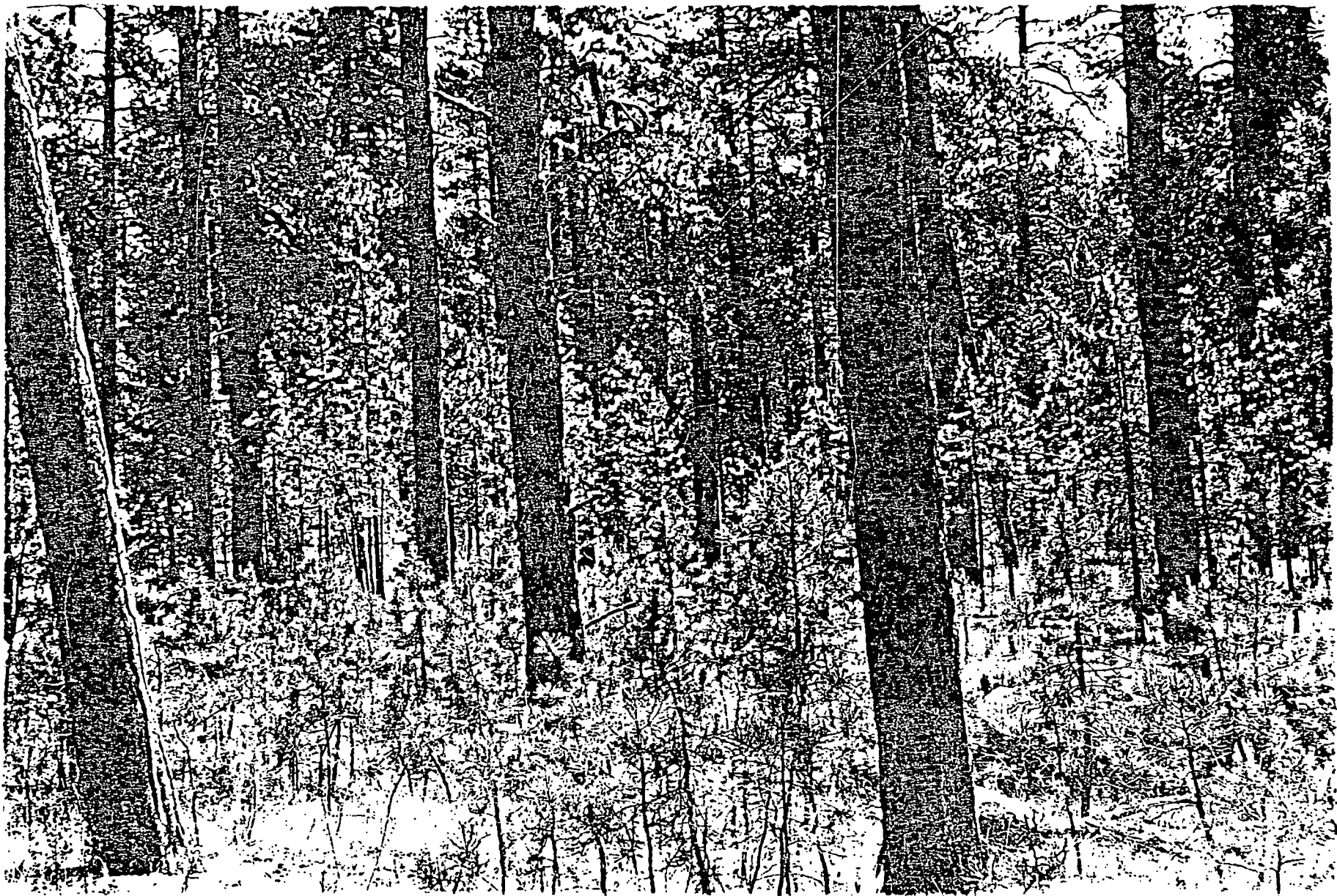


Plate 6. OPEN Plot.





Plate 7. D.H. Plot.



Plate 8. D.H. Plot.



Plate 9. D.H. Plot.

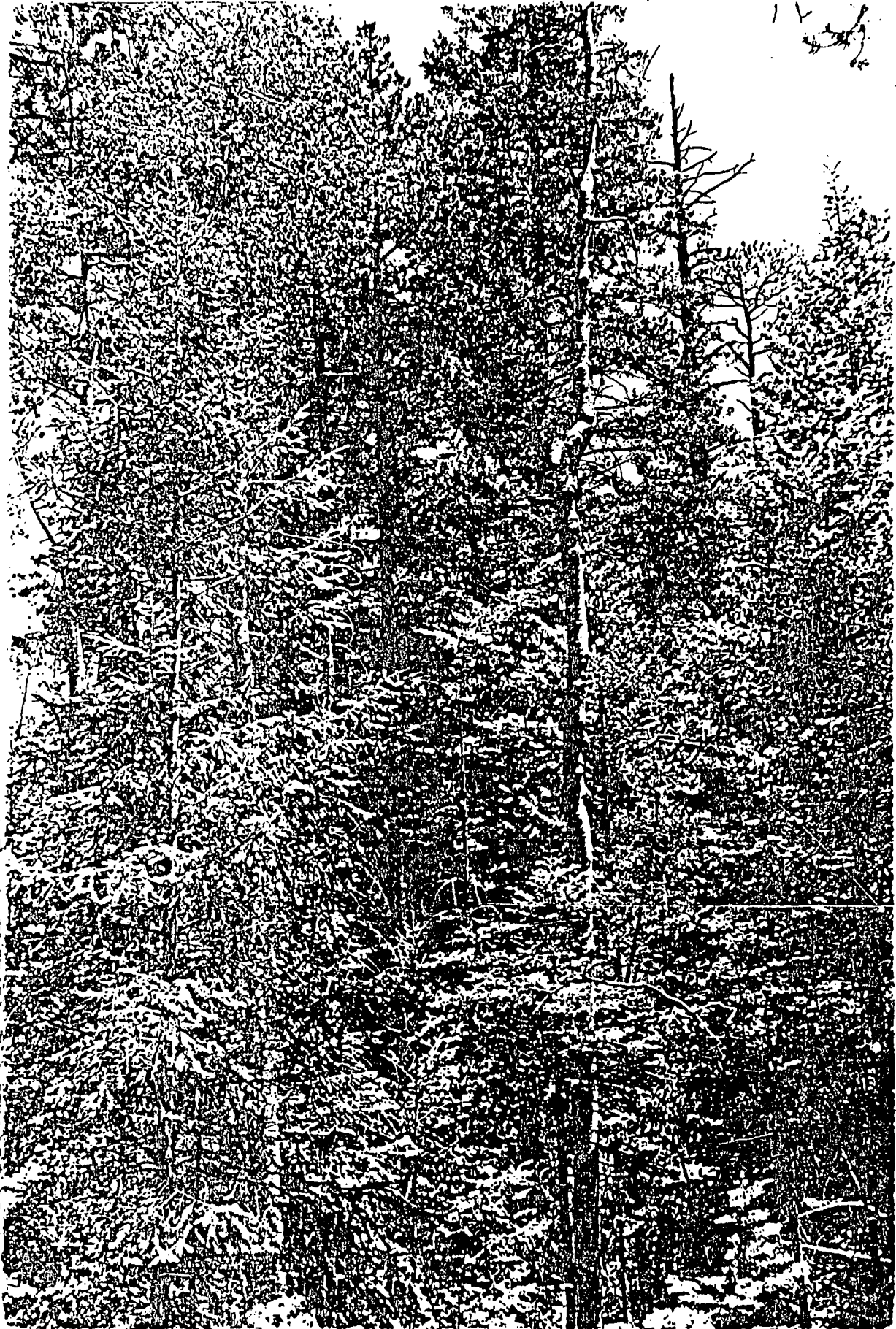


Plate 10. MIX Plot.





Plate 11. MIX Plot.



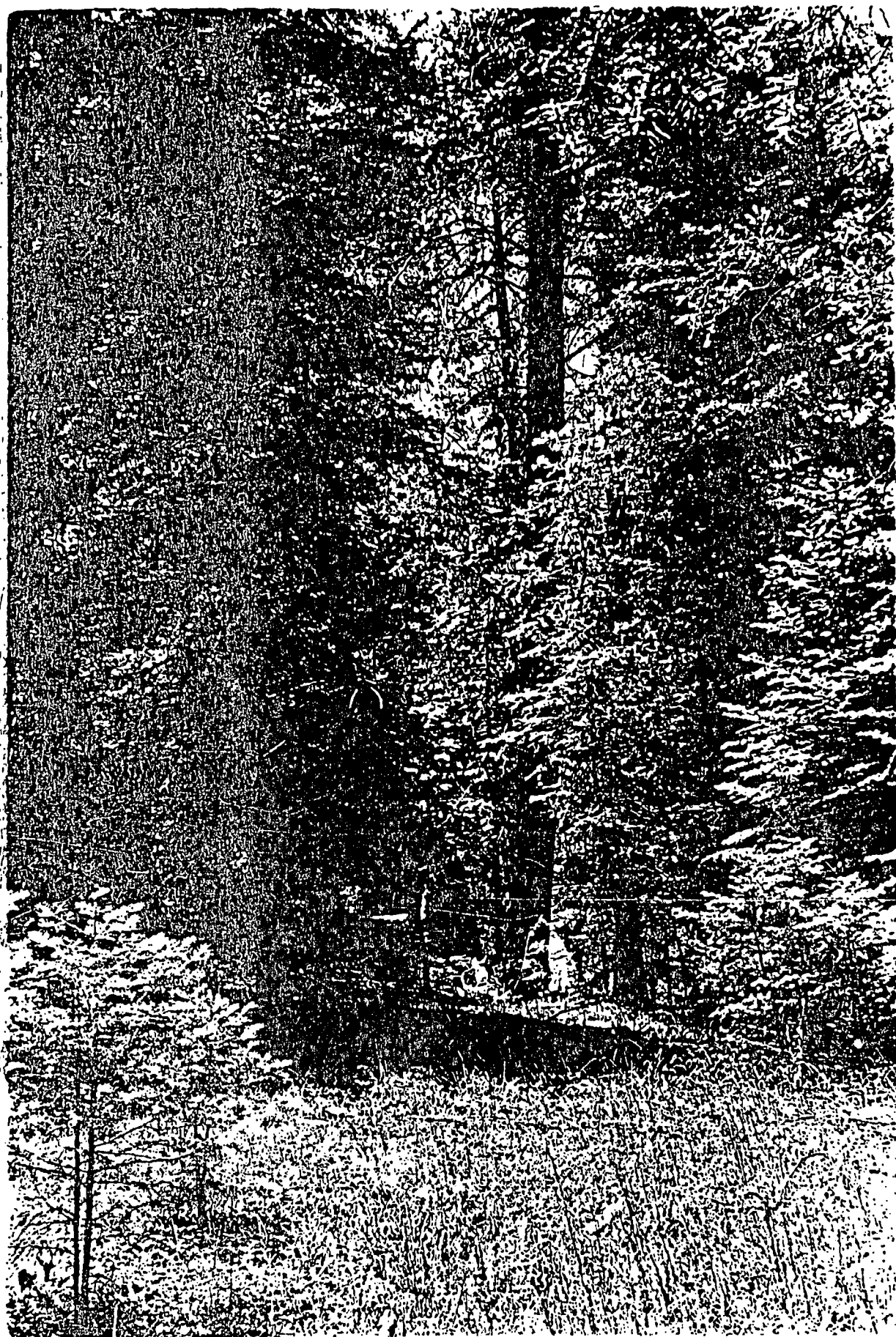


Plate 12. MIX Plot.

Table 1.--Analysis of avifauna of the Jemez Mountains and the MCRNA by continent of origin of families.

Element	Jemez		MCRNA	
	No. of species	%	No. of species	%
Old World	43	36	21	44
North American	29	24	8	16
South American	20	17	9	19
Unanalyzed	<u>27</u>	<u>23</u>	<u>10</u>	<u>21</u>
Total	119	100	48	100

Table 2.--Analysis of avifauna of the Jemez Mountains and the MCRNA by current geographic distribution during the breeding season.

Element	Jemez		MCRNA	
	No. of species	%	No. of species	%
Widespread	51	43	15	31
Boreo-cordilleran	17	14	9	19
Western	26	22	11	23
Southwestern/ Great Basin	7	6	3	6
Cordilleran	11	9	8	17
Mexican	<u>7</u>	<u>6</u>	<u>2</u>	<u>4</u>
Total	119	100	48	100

Table 3.--Birds recorded on the MCRNA, with densities of the species breeding in the plots. The upper value for each species is in prs/8 ha, the lower in prs/100 ha. + = less than 0.5 pr/8 ha. V = visitor.

Species	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Turkey Vulture	V	V	V		
Goshawk	V		V		
Sharp-shinned Hawk		V			
Band-tailed Pigeon	V	V	V		
Mourning Dove		V			
Flammulated Owl					
Great Horned Owl					
Saw-whet Owl					
Common Nighthawk	V			V	
White-throated Swift	V		V		V
Broad-tailed Hummingbird	V	3 37.5	1 12.5	V	
Common Flicker	V	0.5 6.3	1 12.5	0.5 6.3	+
Lewis' Woodpecker					
Williamson's Sapsucker	V	V	1 12.5	+	0.5 6.3
Hairy Woodpecker	V	V	1 12.5	1 12.5	V
N. Three-toed Woodpecker		V	V	V	
Hammond's Flycatcher		V	3 37.5	1 12.5	4.5 56.3
Dusky Flycatcher		3 37.5			

Species	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Western Flycatcher		V			V
Western Wood Pewee	V	6 75			V
Olive-sided Flycatcher		1 12.5			
Violet-green Swallow	1 12.5	1 12.5	2 25	3 37.5	2 25
Steller's Jay		V	+	+	+
Scrub Jay					
Common Raven		V	V		
Clark's Nutcracker	V	V			
Mountain Chickadee	V	V	V	V	1 12.5
White-breasted Nuthatch		0.5 6.3	0.5 6.3	V	+
Pygmy Nuthatch	2 25	2 25	2.5 31.3	3 37.5	1 12.5
Brown Creeper		V	1.5 18.8	1 12.5	1 12.5
House Wren	1 12.5	2 25	2 25		
American Robin		V			
Hermit Thrush	V			2 25	1.5 18.8
Western Bluebird	0.5 6.3	1.5 18.8	1 12.5		+
Townsend's Solitaire	1 12.5	1 12.5	0.5 6.3	V	

Species	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Ruby-crowned Kinglet					2 25
Solitary Vireo	V	3 37.5	2 25	1 12.5	V
Warbling Vireo	V	V	V		1 12.5
Virginia's Warbler		2 25			
Yellow-rumped Warbler	V	0.5 6.3	V	1 12.5	
Grace's Warbler	+	3.5 43.8	2.5 31.3	1 12.5	1 12.5
Brown-headed Cowbird	V				
Western Tanager	V	1.5 18.8			V
Black-headed Grosbeak		1 12.5	V		
Pine Siskin		V	V		
Red Crossbill				V	
Gray-headed Junco	2.5 31.3	1 12.5	2.5 31.3	1 12.5	2.5 31.3
Totals prs/ 8 ha	8	34	24	15.5	18
prs/ 100 ha	100	425	300	193	225
prs/100 acres	40	170	120	78	90
No. of breeding species	7	18	16	13	15
prs/species	1.1	1.9	1.5	1.2	1.2

Table 4.--Number of species and pairs per 100 acres from each Mayrian continental element breeding in the plots. Parenthetical values are percentages.

	Plot				
	THIN	OAK	OPEN	D.H.	MIX
No. of species					
Old World	3(43)	4(22)	6(38)	4(31)	8(53)
North American	3(43)	6(33)	4(25)	4(31)	3(20)
South American		6(33)	2(12)	1(8)	1(7)
Unanalyzed	<u>1(14)</u>	<u>2(11)</u>	<u>4(25)</u>	<u>4(31)</u>	<u>3(20)</u>
Total	7(100)	18(99)	16(100)	13(101)	15(100)
Pairs/100 acres					
Old World	18(44)	25(15)	30(25)	30(39)	33(36)
North American	18(44)	60(35)	45(37)	20(26)	23(25)
South American		78(46)	20(17)	5(6)	23(25)
Unanalyzed	<u>5(13)</u>	<u>8(4)</u>	<u>25(21)</u>	<u>23(29)</u>	<u>13(14)</u>
Total	41(101)	171(100)	120(100)	78(100)	92(100)

Table 5.--Analysis of comparable studies in Ponderosa Pine forests. The upper value for each element is percentage of the total species in the plot. The parenthetical value is percentage of total breeding pairs in the plot.

	Location of study					
	Oregon <sup>1</sup>	central <sup>2</sup>	Colorado <sup>3</sup>	N. Mex. <sup>4</sup>	n. Ariz. <sup>5</sup>	s. Ariz. <sup>6</sup>
No. of spp.	31	20	24	16	23	31
No. prs/100 acres	180	96	68	120	232	336
No. prs/sp.	5.8	4.8	3.1	7.5	10.1	10.8
Elements						
Old World	52 (49)	35 (40)	42 (58)	38 (25)	43 (55)	35 (40)
N. American	13 (25)	45 (39)	29 (23)	25 (37)	17 (18)	26 (36)
S. American	16 (18)	10 (11)	12 (7)	12 (17)	22 (8)	23 (14)

<sup>1</sup>Gashwiler 1977

<sup>2</sup>Hering 1948

<sup>3</sup>Winternitz 1976. Values extrapolated from Tables 1 and 2.

<sup>4</sup>this study, OPEN plot

<sup>5</sup>Haldeman et al. 1973

<sup>6</sup>Balda 1967, as cited in Haldeman et al. 1973



Table 6.--Analysis of comparable studies in mixed coniferous forests. The upper value for each element is percentage of total species in the plot. The parenthetical value is percentage of total breeding pairs in the plot.

	Location of study					
	Calif. <sup>1</sup>	n. Colo. 2	c. Colo. 3	N. Mex. <sup>4</sup>	n. Ariz. <sup>5</sup>	s. Ariz. <sup>6</sup>
No. of spp.	23	16	19	15	27	35
No. prs/100 acres	92	102	58	90	253	367
No. prs/sp.	4.0	6.4	3.2	6.0	9.4	10.7
Elements						
Old World	43 (56)	69 (55)	37 (53)	53 (36)	41 (34)	40 (49)
N. American	22 (25)	13 (40)	26 (28)	20 (25)	19 (31)	23 (31)
S. American	13 (16)	6 (5)	16 (9)	7 (25)	19 (20)	17 (11)

<sup>1</sup>Bock and Lynch 1970

<sup>2</sup>Snyder 1950

<sup>3</sup>Winternitz 1976. Values extrapolated from Tables 1 and 2.

<sup>4</sup>this study, MIX plot.

<sup>5</sup>Haldeman et al. 1973

<sup>6</sup>Franzreb 1977

Table 7.--Number of species and pairs per 100 acres from each geographic element based on current range breeding in the plots. Parenthetical values are percentages.

	Plot				
	THIN	OAK	OPEN	D.H.	MIX
No. of species					
Widespread	1(14)	3(17)	4(25)	2(15)	3(20)
Boreo-cordilleran		3(17)	2(13)	4(31)	3(20)
Western	1(14)	5(28)	3(19)	2(15)	4(27)
Southwestern/ Great Basin	1(14)	2(11)	1(6)	1(8)	1(7)
Cordilleran	3(43)	4(22)	5(31)	3(23)	3(20)
Mexican	<u>1(14)</u>	<u>1(6)</u>	<u>1(6)</u>	<u>1(8)</u>	<u>1(7)</u>
Total	7(99)	18(101)	16(100)	13(100)	15(101)
No. Pairs/100 acres					
Widespread	5(13)	15(9)	23(19)	8(10)	5(6)
Boreo-cordilleran		23(13)	18(15)	25(32)	23(25)
Western	3(6)	65(38)	25(21)	5(6)	30(33)
Southwestern/ Great Basin	13(31)	15(9)	13(10)	5(6)	13(14)
Cordilleran	20(50)	35(21)	30(25)	30(39)	15(17)
Mexican	<u>+</u>	<u>18(10)</u>	<u>13(10)</u>	<u>5(6)</u>	<u>5(6)</u>
Total	41(100)	171(100)	122(100)	78(99)	91(101)

Table 8.--Standing crop biomass of the breeding birds of the plots  
(grams/ 8 ha).

Species	Mean Wgt. (g)	Source <sup>a</sup>	Plot				
			THIN	OAK	OPEN	D.H.	MIX
Broad-tailed Hummingbird	4.0	Sa		24	8		
Common Flicker	145.0	Sa		145	290	145	
Williamson's Sapsucker	54.8	Ha			110		55
Hairy Woodpecker	69.8	Sa			140	140	
Hammond's Flycatcher	10.0	*			60	20	90
Dusky Flycatcher	10.7	Pa		64			
Western Wood Pewee	14.0	Sa		168			
Olive-sided Flycatcher	31.5	Sa		63			
Violet-green Swallow	10.6	Ha	21	21	42	64	42
Steller's Jay	105.0	Ha					
Mountain Chickadee	12.0	Sa					24
White-breasted Nuthatch	20.4	St		20	20		
Pygmy Nuthatch	10.0	Sa	40	40	50	60	20
Brown Creeper	8.0	Sa			24	16	16
House Wren	10.5	Sa	21	42	42		
Hermit Thrush	25.6	Sa				102	77
Western Bluebird	24.6	Ha	25	74	49		
Townsend's Solitaire	32.0	Ha	64	64	32		
Ruby-crowned Kinglet	6.1	Sa					24
Solitary Vireo	16.6	Ha		100	66	33	
Warbling Vireo	11.3	Sa					23

Species	Mean Wgt. (g)	Source <sup>a</sup>	Plot				
			THIN	OAK	OPEN	D.H.	MIX
Virginia's Warbler	9.6	DM		38			
Yellow-rumped Warbler	13.1	Sa		13		26	
Grace's Warbler	7.5	Ha		53	28	15	15
Western Tanager	29.0	Sa		87			
Black-headed Grosbeak	46.0	Sa		92			
Gray-headed Junco	20.3	Ha	<u>102</u>	<u>41</u>	<u>102</u>	<u>41</u>	<u>102</u>
Total (g/8 ha)			273	1149	1073	662	488
(g/ha)			34	143	134	83	61

<sup>a</sup>Ha = Haldeman et al. 1973, Pa = Pache 1975, Sa = Salt 1957, St = Stewart 1937, DM = Denver Museum of Natural History, \* = no specimen available -- estimate.

Table 9.--Number of breeding pairs of each size class in the plots.  
 Parenthetical values are percentages.

	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Tiny	2(25)	10.5(31)	10.5(44)	6(39)	9.5(53)
Small	5(63)	18.5(54)	10.0(42)	6(39)	6.5(36)
Medium	1(12)	4.5(13)	2.5(10)	3(19)	2.0(11)
Large		.5(1)	1.0(4)	.5(3)	
Total	7(100)	34.0(99)	24.0(100)	15.5(100)	18.0(100)



Table 12.--Importance of avian species in the MCRNA, as reckoned by summed dominance rankings.

Rank	Species	<u>Numbers</u>	Imp. value	Rank	Species	<u>Biomass</u>	Imp. value
1.	Hammond's Flycatcher		4	1.	Common Flicker		5
2.	Gray-headed Junco		3.3	2.	Gray-headed Junco		4
3.	Pygmy Nuthatch		2.8	3.	Western Wood Pewee		2
4.	Western Wood Pewee		2	4.	Hairy Woodpecker		2
5.	Violet-green Swallow		1.5	5.	Townsend Solitaire		1
6.	Grace's Warbler		1.3	6.	Hammond's Flycatcher		1
Rank	Species	<u>Combined</u>	Imp. value				
1.	Gray-headed Junco		7.7				
2.	Hammond's Flycatcher		5				
3.	Common Flicker		5				
4.	Western Wood Pewee		4				
5.	Pygmy Nuthatch		2.8				
6.	Hairy Woodpecker		2				
7.	Violet-green Swallow		1.5				
8.	Grace's Warbler		1.3				
9.	Townsend's Solitaire		1				

Table 13.--Matrix of similarity based on the formula  $FRF = 2C / A + B$ .  
 Values on the upper right are the similarity indices.  
 Values on the lower left are C. Marginal values are the  
 species counts for the plots.

	THIN 7	OAK 18	OPEN 16	D.H. 13	MIX 15
THIN 7		.560	.609	.400	.455
OAK 18	7		.647	.452	.424
OPEN 16	7	11		.759	.710
D.H. 13	4	7	11		.714
MIX 15	5	7	11	10	



Table 14.--Matrix of similarity based on the formula  $IS = 2\sum W / A + B$ .  
 Values on the upper right are the similarity indices.  
 Values on the lower left are  $\sum W$ . Marginal values are  
 population densities for the plots.

	THIN 8.0	OAK 34.0	OPEN 24.0	D.H. 15.5	MIX 18.0
THIN 8.0		.306	.469	.340	.346
OAK 34.0	6.5		.483	.263	.135
OPEN 24.0	7.5	14.0		.557	.524
D.H. 15.5	4.0	6.5	11.0		.507
MIX 18.0	4.5	3.5	11.0	8.5	

Table 15.--Matrix of similarity based on "percentage similarity" =  
1 - percentage difference (Odum 1950).

	THIN	OAK	OPEN	D.H.	MIX
THIN		.318	.438	.340	.250
OAK			.487	.290	.162
OPEN				.557	.560
D.H.					.508
MIX					

Table 16.--Ranks of plot dyads in the similarity matrices.

Table 15. (Odum)	Rank in Table 13. (FRF)	Rank in Table 14. (IS)
1. OPEN/MIX	3	2
2. OPEN/D.H.	1	1
3. D.H./MIX	2	3
4. OAK/OPEN	4	4
5. THIN/OPEN	5	5
6. THIN/D.H.	10	7
7. THIN/OAK	6	8
8. OAK/D.H.	8	9
9. THIN/MIX	7	6
10. OAK/MIX	9	10

Table 17.--Nesting and foraging guilds of the species breeding on the plots.

NEST FORAGING	CAVITY-I	CAVITY-II	FOLIAGE- CANOPY	FOLIAGE- UNDERSTORY	FOLIAGE- SHRUB	GROUND
NECTAR					Broad-tailed Hummingbird	
AERIAL		Violet-green Swallow				
HAWK (Fly- catching)			Olive-sided Flycatcher	Hammond's Flycatcher W. Wood Pewee	Dusky Flycatcher	
TIMBER- DRILL	Williamson's Sapsucker Hairy Wood- pecker					
TIMBER- PROBE	White-breasted Nuthatch Pygmy Nuthatch	Brown Creeper				
FOLIAGE- INSECT		Mountain Chickadee House Wren	Ruby-crowned Kinglet Yellow-rumped Warbler Grace's Warbler	Steller's Jay Solitary Vireo Warbling Vireo Western Tanager Black-headed Grosbeak		Virginia's Warbler
GROUND- INSECT	Common Flicker	Western Blue- bird		Hermit Thrush		Townsend's Solitaire Gray-headed Junco

Table 18.--Densities and biomass of the foraging guilds on the plots.  
 Parenthetical values are percentages.

Guild	<u>DENSITY (prs/ 8 ha)</u>				
	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Aerial	1.0(13)	1.0(3)	2.0(8)	3.0(19)	2.0(11)
Hawk		10.0(29)	3.0(13)	1.0(7)	4.5(25)
Timber-Drill			2.0(8)	1.0(7)	0.5(3)
Timber-Probe	2.0(25)	2.5(7)	4.5(19)	4.0(26)	2.0(11)
Foliage-Insect	1.0(13)	13.5(40)	6.5(27)	3.0(19)	4.0(22)
Ground-Insect	4.0(50)	4.0(12)	5.0(21)	3.5(23)	5.0(28)
Nectar		3.0(9)	1.0(4)		
Total	8.0(101)	34.0(100)	24.0(100)	15.5(101)	18.0(100)
	<u>BIOMASS (g/8 ha)</u>				
	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Aerial	21(8)	21(2)	42(4)	64(10)	42(9)
Hawk		295(26)	60(6)	20(3)	90(18)
Timber-Drill			249(23)	140(21)	55(11)
Timber-Probe	40(15)	60(5)	94(9)	76(11)	36(7)
Foliage-Insect	21(8)	424(37)	146(14)	74(11)	62(13)
Ground-Insect	190(70)	323(28)	473(44)	288(44)	202(41)
Nectar		24(2)	8(1)		
Total	272(101)	1147(100)	1072(101)	662(100)	487(99)

Table 19.--Densities and biomass of the nesting guilds on the plots.  
 Parenthetical values are percentages.

Guild	<u>DENSITY (prs/ 8 ha)</u>				
	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Cavity-I	2.0(25)	3.0(9)	6.0(25)	4.5(29)	1.5(8)
Cavity-II	2.5(31)	4.5(13)	6.5(27)	4.0(26)	4.0(22)
Foliage-Canopy	+	5.0(15)	2.5(10)	2.0(13)	3.0(17)
Foliage-Understory		11.5(34)	5.0(21)	4.0(26)	7.0(39)
Foliage Shrub		6.0(18)	1.0(4)		
Ground	3.5(44)	4.0(12)	3.0(13)	1.0(7)	2.5(14)
Total	8.0(100)	34.0(101)	24.0(100)	15.5(100)	18.0(100)

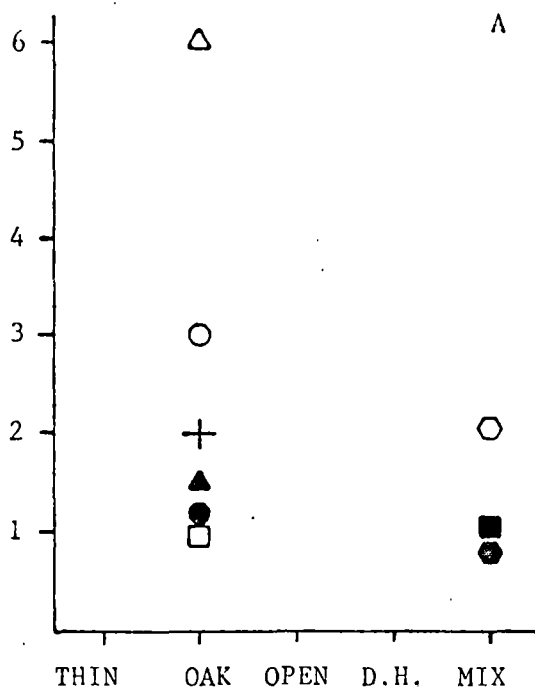
Guild	<u>BIOMASS (g/8 ha)</u>				
	Plot				
	THIN	OAK	OPEN	D.H.	MIX
Cavity-I	40(15)	205(18)	610(57)	345(52)	75(15)
Cavity-II	67(25)	137(12)	158(15)	80(12)	82(17)
Foliage-Canopy		129(11)	38(4)	41(6)	39(8)
Foliage-Understory		447(39)	126(12)	156(24)	189(39)
Foliage-Shrub		88(8)	8(1)		
Ground	166(61)	143(12)	134(12)	41(6)	102(21)
Total	272(101)	1149(100)	1073(101)	662(100)	488(100)

Table 20.--Number of snags and cavity-nesting birds in each plot.

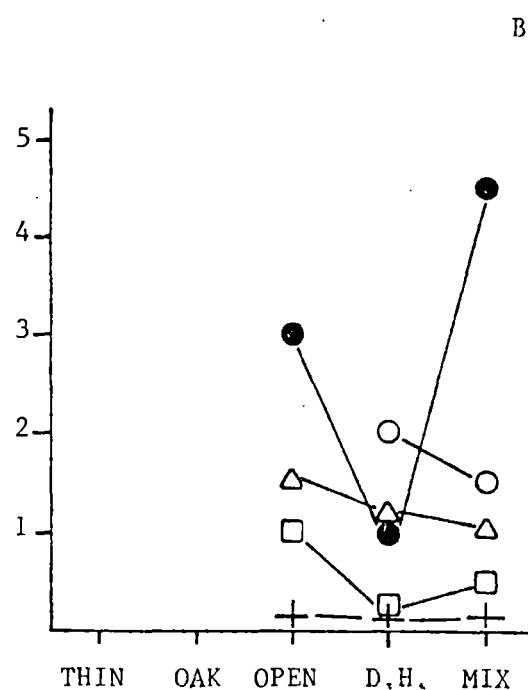
Plot	Snags	No. of cavity-nesters
THIN	10	4.5
OAK	25	7.5
OPEN	22	12.5
D.H.	62	8.5
MIX	63	5.5

Figure 1.--Gradient analysis of populations. Densities, in pairs/ 8 ha, appear on the vertical axis. Plots are on the horizontal axis.

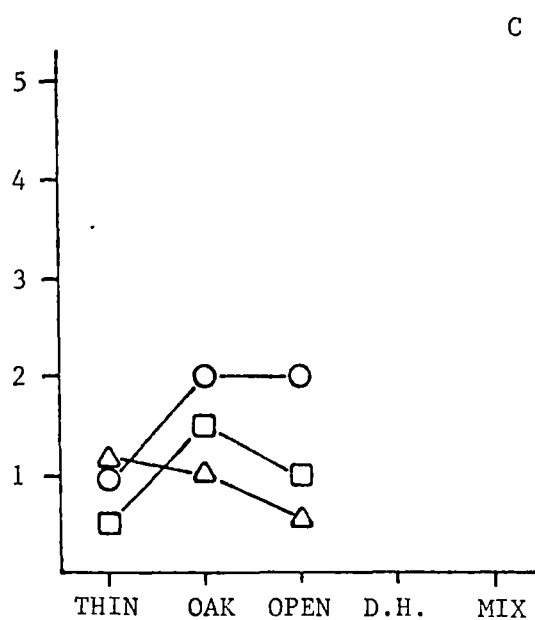




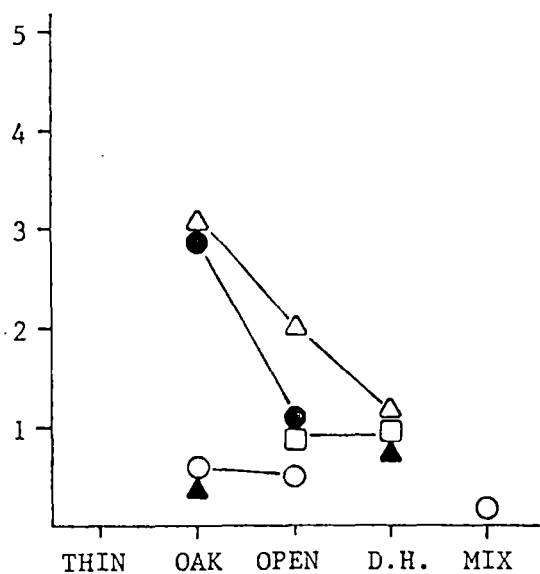
- △ Western Wood Pewee
- ▲ Western Tanager
- Dusky Flycatcher
- Black-headed Grosbeak
- Olive-sided Flycatcher
- Warbling Vireo
- Ruby-crowned Kinglet
- Mountain Chickadee
- + Virginia's Warbler



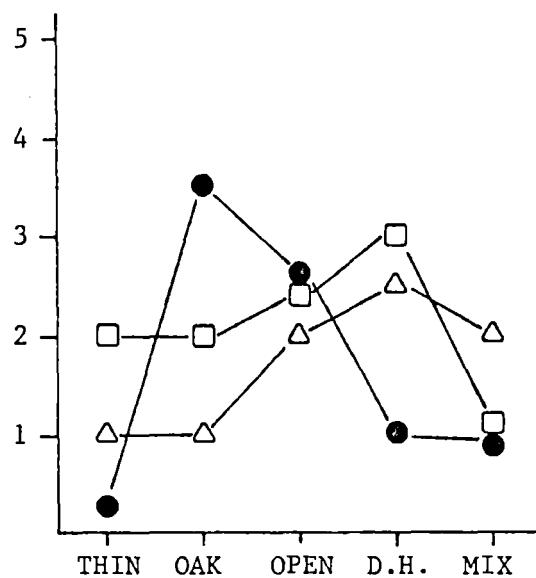
- △ Brown Creeper
- Hermit Thrush
- Hammond's Flycatcher
- Williamson's Sapsucker
- + Steller's Jay



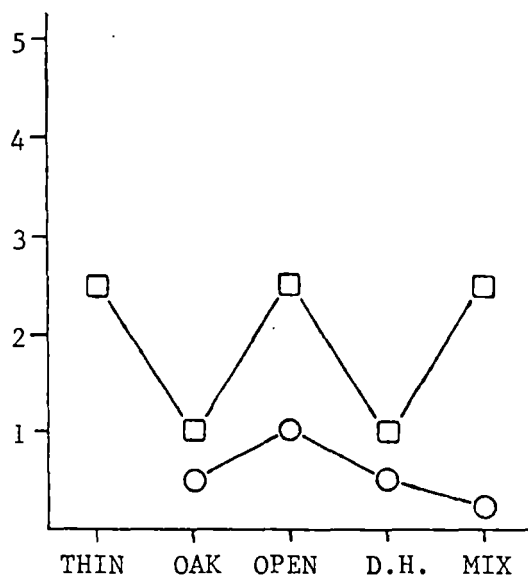
- △ Townsend's Solitaire
- House Wren
- Western Bluebird



- △ Solitary Vireo
- ▲ Yellow-rumped Warbler
- White-breasted Nuthatch
- Broad-tailed Hummingbird
- Hairy Woodpecker



- △ Violet-green Swallow
- Grace's Warbler
- Pygmy Nuthatch



- Common Flicker
- Gray-headed Junco

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## APPENDIX I

## ANNOTATED CHECKLIST

Turkey Vulture (Cathartes aura). Seen occasionally over the RNA.

Goshawk (Accipiter gentilis). Seen twice in June.

Sharp-shinned Hawk (Accipiter stratus). Seen July 13.

Band-tailed Pigeon (Columba fasciata). First seen 30 May, and irregularly thereafter. This species breeds in late summer and early fall and may have nested in the MCRNA.

Mourning Dove (Zenaida macroura). Heard once, on June 22. The Mourning Dove sometimes breeds in coniferous forest, and at elevations higher than the MCRNA's.

Flammulated Owl (Otus flammeolus). First heard April 30, and frequently thereafter through May. At 2055 MDT on May 16 one flew before my headlights, about 1.5 m off the ground. I switched off the ignition and heard it hooting a short distance away within the thicket.

Great Horned Owl (Bubo virginianus). Seen east of the MCRNA in June and heard in Monument Canyon in October, 1978.

Saw-whet Owl (Aegolius acadicus). Heard frequently, late at night, in April and May, in dense forest.

Common Nighthawk (Chordeiles minor). First heard May 29. Thereafter heard and seen frequently at dusk over the RNA.

White-throated Swift (Aeronautes saxatilis). Common over all parts of the RNA. Probably nested in the steep cliffs on the north edge of the section.

Broad-tailed Hummingbird (Selasphorus platycercus). Fairly common. Difficult to census because males are promiscuous. Nevertheless I used loci of male activity to delimit "territories" in OAK.

Common Flicker (Colaptes auratus). Difficult to census because of largeness of territories. Displays involving more than one member of either sex were considered to take place near boundaries. Such a display last noted on June 1. A female ejected sawdust from the only known nest on May 3. Juveniles were seen in the same territory on July 13.

Lewis' Woodpecker (Melanerpes lewis). Seen on May 16 in open pine woodland.

Williamson's Sapsucker (Sphyrapicus thyroideus). Conspicuous, but the extent of territories was difficult to assess because of their large sizes. Foraged in open pine forest, but each territory included some aspens, which are greatly favored by the species for nesting sites. A presumed territorial dispute involving two females and one male was observed on April 21. A pair copulated and inspected a hole in an aspen on May 29.

Hairy Woodpecker (Picoides villosus). This species also has large territories and is accordingly difficult to census. A pair was feeding young in a nest in an aspen on June 21. A juvenile with an adult was seen in another area on July 12.

Northern Three-toed Woodpecker (Picoides tridactylus). Rather frequently seen in tall trees throughout the RNA, but not recorded as breeding on any plot. Two males, with a female in company, displayed at each other on June 22 in open pine forest.

Hammond's Flycatcher (Empidonax hammondi). This species sings vociferously before dawn, and its small territories are consequently fairly easy to delimit. In the MCRNA it occupies areas with a tall overstory and moderately dense subcanopy. More open forest with a shrub layer is occupied by the Dusky Flycatcher. A nest was being built on a short dead limb of a ponderosa pine, about 30 feet above the ground, on May 29. According to the literature this is a typical height for a Hammond's Flycatcher nest. While foraging this species ranged from the bottom of the canopy to ground level. It was frequently seen quite close to the ground.

Dusky Flycatcher (Empidonax oberholseri). This species was restricted to the OAK plot and similar vegetation. It was less conspicuous than E. hammondi, and thus somewhat more difficult to census, but the linear arrangement of the territories in the narrow strip of appropriate vegetation somewhat ameliorated this difficulty. I never encountered this species outside the pine-oak vegetation belt, and only once did E. hammondi ascend the slope above OPEN and enter a dusky territory. A nest was under construction on June 1, and another held four eggs on June 21. Both were in crotches of scrub oaks, less than 2 m above the ground.

Western Flycatcher (Empidonax difficilis). The Western Flycatcher was vociferous in two places outside the plots, but I was unable to assess its breeding status or its habitat preference.

Western Wood Pewee (Contopus sordidulus). Kilgore (1971) showed that this species responds positively to opening dense understory vegetation. It used similar habitat in the MCRNA, hawking insects in the open airspace between the canopy and scrub oaks in OAK and places with similar characteristics. Pewees can be quite abundant in suitable habitat, as they were here. The difficulty of distinguishing between intra-pair and territorial hostility complicates censusing.

Olive-sided Flycatcher (Nuttallornis borealis). This is generally thought to be a bird of tall trees in boreal forests, so it was surprising to find it in OAK. Apparently isolated snags and steep slopes are the cues by which it chooses territories for these are the only discerned as common between OAK and the mixed coniferous forest of the northern edge of the RNA, the two places where I found the species.

Violet-green Swallow (Tachycineta thalassina). This, the only swallow seen in the RNA, was ubiquitous in the airspace above the trees. Because they are aerial foragers the only structural characteristic of habitat which limits numbers is nest sites. I saw only scant evidence of nesting before June 22, when swallows in several areas were busily gathering nesting material from the ground, so the season may have been retarded. I only spent two days after this date, July 12-13, at the RNA, and although my chief objective during those days was finding swallow nests it is quite possible I underestimated their numbers. Nevertheless, as I exerted approximate equal efforts in all plots the relative abundances are probably correct. I found seven nests, three in dead pines, two in living pines, and two in aspens.

Steller's Jay (Cyanocitta stelleri). Steller's Jays present great difficulties to the census-taker. They occupy large home ranges with other pairs, only defending small areas around their nests. Furthermore, they are extremely stealthy in the vicinity of their nests. For these reasons I did not feel justified in attempting density estimates for this species, and merely recorded them as present (+) in the three plots where I saw them frequently.

Scrub Jay (Aphelocoma coerulescens). Seen once near THIN.

Common Raven (Corvus corax). Common over the plots, but appropriate nesting cliffs do not exist in them. May nest in cliffs on north edge of RNA.

Clark's Nutcracker (Nucifraga columbiana). Seen on May 30 and June 21. This species nests in early spring near timberline and disperses downhill afterward.

Mountain Chickadee (Parus gambeli). This is usually a very common species in coniferous forests. Presumably it suffered a population crash in the winter of 1978-79, for it was decidedly rare throughout the MCRNA during this study. In a typical year it would be expected to nest in all five plots.

White-breasted Nuthatch (Sitta carolinensis). These nuthatches occupy very large territories. As a result boundary disputes are infrequent and boundaries are difficult to map. In this case it was easy to determine how many pairs occupied a plot, but very difficult to estimate how much of each territory was in a plot. These birds prefer relatively open forests.

Pygmy Nuthatch (Sitta pygmaea). This was the most conspicuous species on the MCRNA, both in winter, when large flocks coursed through the "dog-hair" stands, and in summer. Territories are not very clearly delimited, but occupied areas become evident in time because of the frequent calling of this species. Additionally, nests are relatively easy to find during the excavation period. These birds eschewed the denser parts of the MIX plot and similar vegetation, but were otherwise ubiquitous. Four nests were found, all in dead pines. This is one of the few cavity-nesters that has little use for aspens.

Brown Creeper (Certhia familiaris). The creeper sings fairly conspicuously early in the breeding season, and is thus relatively easy to census. They seem to have rather large territories for a species of small body-size. Dead or dying trees are required by this species, for they nest under slabs of exfoliating bark.

House Wren (Troglodytes aedon). House Wrens are quite noisy and have small territories. They are relatively easy to census. They are very aggressive and have been known to expel larger occupants from desired nest cavities. I infer that the piles of slash in THIN were adequate man-made substitutes for the shrubs or piles of brush which these wrens typically frequent. Three nests were found, two in pine stubs, and one in a dead aspen.

American Robin (Turdus migratorius). The robin was only seen once the entire breeding season. The absence of such a common and widespread species demands explanations. The only simple one is that unavailability of mud, an essential nest-building material, discourages it from using the RNA. Robins do build nests without mud, but it is a favored material. They are most common where it is available, as Hering's study (1948) clearly showed.

Hermit Thrush (Catharus guttatus). In the study area the Hermit Thrush was restricted to areas with deep shade and tall trees, from which males sang at dusk and before dawn. The species was regular in "dog-hair" stands. One nest was found, in an aspen in the MIX plot.

Western Bluebird (Sialia mexicana). This species is difficult to census unless nests are found, because individuals range into different kinds of vegetation to forage. This phenomenon is well-illustrated by a pair which nested in a tall pine in a "dog-hair" stand, where their style of foraging is impossible, and foraged in the adjacent THIN plot, where nest sites were rare. The two other nests found were both in aspens. One of these was in a tree also occupied by a pair of Violet-green Swallows and a pair of Williamson's Sapsuckers. This tree was on a boundary between dense mixed coniferous forest, where none of these species could forage effectively, and more open pine forest. At the third nest both bluebirds attacked and fought a neighboring Hairy Woodpecker whenever he came close to their tree.

Townsend's Solitaire (Myadestes townsendi). Male solitaires do much of their singing from the air, where their positions are difficult to locate. This makes mapping difficult. Their territories seem to be large. This species has been found by other workers in mixed coniferous forests, so its limitation to the more open stands in the MCRNA does not imply a strict habitat requirement. One nest was found, under a burned stump.

Ruby-crowned Kinglet (Regulus calendula). Kinglets were present, and even sang, in pinewoods during the spring. However, these birds were migrants. The only areas from which singing persistently emanated throughout the study were in the densest groves of mixed conifers. Censusing these males was not difficult. This species had perhaps the strictest habitat requirement of any species in the study.

Solitary Vireo (Vireo solitarius). These birds sing incessantly, even well into the incubation period. Singing males also approach each other. These habits make delimitation of territories rather easy. The one nest found was about 4 m high in a pine sapling, in a relatively open area in D.H. On June 19 it held three almost-grown nestlings.

Warbling Vireo (Vireo gilvus). Warbling vireos appeared in the MCRNA on the late date of May 29, as is typical of the species. Eventually two pairs claimed territories, both in stands of aspens.

Virginia's Warbler (Vermivora virginiae). This species was limited to areas with dense stands of scrubby oaks. It nests among the roots of the oaks and forages and sings from their branches. Censusing presented no special difficulties.

Yellow-rumped Warbler (Dendroica coronata). The Yellow-rumped Warbler is frequently abundant in coniferous forests, but it was decidedly uncommon on the MCRNA in 1979. For this reason its habitat requirements cannot be inferred from the results of this study. This species is usually thought of as favoring the upper reaches of trees (Franzreb 1977), but in the MCRNA both sexes foraged and males sang within 3 m of the ground frequently, especially in May. This was especially noticeable in "dog-hair" thickets, which the species seemed to favor.

Grace's Warbler (Dendroica graciae). This is an abundant species in the MCRNA. They were usually encountered high in pines. It is conceivable that the abundance of these birds has caused the Yellow-rumped Warbler to adjust its foraging zone downward because of interaction with Grace's Warblers. Marshall (1957) considered D. graciae dominant over D. coronata. Males from contiguous territories often sang simultaneously, facilitating the mapping of their territories.

Brown-headed Cowbird (Molothrus ater). Seen three times, twice near THIN and once in OAK.

Western Tanager (Piranga ludoviciana). Recorded in all habitat-types along the gradient, but frequently enough for listing as a breeding bird only in OAK. One sang often in an open pine forest like that represented in OPEN. This species is more variable in habitat selection than the results of this study imply.

Black-headed Grosbeak (Pheucticus melanocephalus). The Black-headed Grosbeak occurs in riparian deciduous woodlands as well as in coniferous forests. It seems to favor areas with some deciduous vegetation. Perhaps broad-leaved species make better nest sites.

Pine Siskin (Carduelis pinus). Seen on June 1 in OPEN.

Red Crossbill (Loxia curvirostra). Seen on July 12.

Gray-headed Junco (Junco caniceps). A ubiquitous and common species. A nest with newly-hatched nestlings was found under a tussock of grass on June 19 in THIN.

## APPENDIX II

Hypothetical breeding avifauna of the Jemez Mountains, with assignments to faunistic elements on the basis of continent of origin and current range. OW = Old World, NA = North American, SA = South American, Un = Unanalyzed, Wi = Widespread, BC = Boreo-cordilleran, We = Western, SG = Southwestern/Great Basin, Co = Cordilleran, Mx = Mexican.

Species	Cont. of Origin	Current Range	Species	Cont. of Origin	Current Range
Turkey Vulture	NA	Wi	Dusky Flycatcher	SA	We
Goshawk	Un	BC	Gray Flycatcher	SA	SG
Sharp-shinned Hawk	Un	Wi	Western Flycatcher	SA	Co
Cooper's Hawk	Un	Wi	Western Wood Pewee	SA	We
Red-tailed Hawk	Un	Wi	Olive-sided Flycatcher	SA	BC
Zone-tailed Hawk	Un	Mx	Violet-green Swallow	Un	Co
Golden Eagle	Un	Wi	Tree Swallow	Un	Wi
Prairie Falcon	Un	We	Bank Swallow	Un	Wi
Peregrine Falcon	Un	Wi	Rough-winged Swallow	Un	Wi
American Kestrel	Un	Wi	Barn Swallow	Un	Wi
Blue Grouse	NA	Co	Cliff Swallow	Un	Wi
Wild Turkey	NA	Wi	Purple Martin	Un	Wi
Band-tailed Pigeon	OW	Mx	Gray Jay	OW	BC
Mourning Dove	OW	Wi	Steller's Jay	OW	Co
Barn Owl	OW	Wi	Scrub Jay	OW	We
Screech Owl	OW	Wi	Common Raven	OW	Wi
Flammulated Owl	OW	Co	Common Crow	OW	Wi
Great Horned Owl	OW	Wi	Pinyon Jay	OW	SG
Pygmy Owl	OW	Co	Clark's Nutcracker	OW	Co
Spotted Owl	OW	Mx	Mountain Chickadee	OW	Co
Long-eared Owl	OW	Wi	Plain Titmouse	OW	We
Saw-whet Owl	OW	Wi	Bushtit	OW	We
Poor-will	Un	We	White-breasted Nuthatch	OW	Wi
Common Nighthawk	Un	Wi	Red-breasted Nuthatch	OW	BC
White-throated Swift	Un	Co	Pygmy Nuthatch	OW	Co
Broad-tailed Hummingbird	SA	Co	Brown Creeper	OW	BC
Belted Kingfisher	OW	Wi	Dipper	NA	Co
Common Flicker	Un	Wi	House Wren	NA	Wi
Acorn Woodpecker	Un	Mx	Bewick's Wren	NA	Wi
Lewis' Woodpecker	Un	We	Canyon Wren	NA	We
Yellow-bellied Sapsucker	Un	BC	Rock Wren	NA	We
Williamson's Sapsucker	Un	We	Northern Mockingbird	NA	Wi
Hairy Woodpecker	Un	Wi	Gray Catbird	NA	Wi
Downy Woodpecker	Un	Wi	American Robin	OW	Wi
N. Three-toed Woodpecker	Un	BC	Hermit Thrush	OW	BC
Western Kingbird	SA	Wi	Swainson's Thrush	OW	BC
Cassin's Kingbird	SA	Mx	Western Bluebird	OW	We
Ash-throated Flycatcher	SA	We	Mountain Bluebird	OW	Co
Say's Phoebe	SA	WE	Townsend's Solitaire	OW	Co
Hammond's Flycatcher	SA	WE	Blue-gray Gnatcatcher	NA	Wi

Species	Cont. of Origin	Current Range
Golden-crowned Kinglet	OW	BC
Ruby-crowned Kinglet	OW	BC
Starling	OW	Wi
Solitary Vireo	NA	BC
Warbling Vireo	NA	Wi
Orange-crowned Warbler	NA	We
Virginia's Warbler	NA	SG
Yellow Warbler	NA	Wi
Yellow-rumped Warbler	NA	BC
Black-throated Gray Warbler	NA	SG
Grace's Warbler	NA	Mx
MacGillivray's Warbler	NA	We
House Sparrow	OW	Wi
Yellow-headed Blackbird	SA	We
Red-winged Blackbird	SA	Wi
Northern Oriole	SA	Wi
Brewer's Blackbird	SA	We
Brown-headed Cowbird	SA	Wi
Western Tanager	SA	We
Hepatic Tanager	SA	Mx
Black-headed Grosbeak	SA	We
Lazuli Bunting	SA	We
Evening Grosbeak	OW	BC
Cassin's Finch	OW	We
House Finch	OW	We
Pine Grosbeak	OW	BC
Pine Siskin	OW	BC
American Goldfinch	OW	Wi
Lesser Goldfinch	OW	We
Red Crossbill	OW	Wi
Green-tailed Towhee	NA	SG
Rufous-sided Towhee	NA	Wi
Brown Towhee	NA	SG
Vesper Sparrow	NA	Wi
Gray-headed Junco	NA	SG
Chipping Sparrow	NA	Wi
White-crowned Sparrow	NA	Wi
Lincoln's Sparrow	NA	BC
Song Sparrow	NA	Wi